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FURTHER OBSERVATIONS ON THE INNERVATION OF THE TEETH AND THE FIBRES OF MUMMERY

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In a previous paper(2), an account was given of an investigation into the nerve supply of the dentinal tissues. The structures more particularly studied were a certain group of fibres which the late J. Howard Mummery had claimed to be of nervous origin. In his earlier papers on this subject that author had described these structures as arising from the plexus of Raschkow, and then running outwards between the odontoblasts to end in the dentine. It is to be noted that Raschkow's plexus is situated at the base of the layer of the odontoblasts, and that Mummery stated that it was formed from the terminal fibres of the dentinal branches of the trigeminal nerve. In his later papers Mummery modified his views to a certain extent, and now stated that the nerve fibres for the dentine did not arise directly from the plexus, but were the axon cylinders of special nerve cells which were placed at the base of the odontoblast layer, on the peripheral side of Raschkow's plexus. He described these cells as having dendrites which established synaptic connections with the fibres of the plexus.

In the paper referred to above, it was shown that the sub-odontoblastic cells of Mummery do not exist. It was also demonstrated that the fibres, which he described, are not the terminal fibres of the dental branches of the trigeminal nerve. This was proved by cutting the inferior dental nerve in a number of cats, just before it entered the jaw at the inferior dental foramen. After the operation the animals were allowed to live for periods varying from two to four weeks, so that the nerve might degenerate, and then killed. The four posterior teeth of both sides of the lower jaw were removed, fixed in formol, decalcified with formic acid, sectioned with a freezing microtome, and finally stained by the Beckwith gold chloride method and mounted in Euparal. The preparations from the left or denervated side were then compared with those from the right or normal side, and it was found that the fibres of Mummery were just as numerous and distinct on the left as on the right side, which could not have occurred if they had been the terminal fibres of the degenerated nerve.

These results go a long way towards establishing the proposition that Mummery's fibres are not nerves. It could be argued, however, that as there is a sympathetic plexus around the inferior dental artery, which supplies the teeth, and it was not divided in the experiments, therefore the possibility has not been completely eliminated of Mummery's fibres being nerves arising from

the periarterial plexus. It was with the object of clearing up this point that the investigation about to be described was carried out.

The procedure adopted was very similar to that which was used in the earlier investigation. Cats were again the animals chosen, and in each case the inferior dental artery and nerve was divided in a series of subjects. Periarterial sympathectomy was not attempted on account of the small size of the artery, and its position, which would have rendered the performance of the operation, in a satisfactory manner, a matter of great difficulty. The only way left therefore of cutting off the periarterial nerve supply was the one resorted to, of division and ligature of the artery itself. By using this technique there was however the possiblity that a fallacy might arise, from the fact of the sudden cutting off of the blood supply to the teeth. This might so damage the tissues of the pulp, that the fibres of Mummery might disappear from that cause alone.

To gain some idea of the effects of ligaturing the inferior dental artery, the operation was carried out in a second series of cats, four in number, where the left artery was ligatured and divided, while the nerve was left intact. During the last few weeks, several months after the experiments were commenced, a paper by Euler (1) was found, in which he described the results of a series of experiments in which he had performed the same operation in a number of animals.

It may be permissible at this point to digress for a few moments, to discuss Euler's work. He carried out most of his experiments on very young cats, in which the teeth were only developing; he also, however, included an older dog as a control. He found on examining his specimens, that at the end of a fortnight the blood supply to the pulps of the teeth and tissues of the jaw generally had returned to normal. The jaw was now as richly supplied with blood on the operated side, as on the unoperated one. This result he believed to be due to free anastomatic connections between the dental artery and the facial and lingual arteries. The effect of the complete re-establishment of the blood supply to the teeth, both developing and fully grown, was such that any histological changes which might have taken place in the tissues of the pulp entirely disappeared within the fortnight after the operation. On microscopic examination it was impossible to differentiate between the dentinal pulps of the two halves of the jaw. In only one structure were changes of a more permanent nature found, and this was in the inferior dental nerve. Here many of the axon cylinders were markedly affected, some of them were swollen, some shrunken, and others had disappeared. The regeneration of these fibres took place very slowly.

In the present investigation it has been possible, in mature animals with fully developed teeth, to confirm certain of Euler's conclusions. It was found that in those animals which had been allowed to live for over three weeks, there was little to distinguish the pulps of one side from those of the other. This is clearly shown in figs. 1 and 2, which are micro-photographs of trans-

verse sections of the right and left molar teeth respectively of a cat, which was permitted to survive for 29 days after the left inferior dental artery had been divided. The sections, which were stained with haemalum and eosin, and mounted in balsam, show that the pulp tissue on the side which was operated upon presents no histological features by which it can be distinguished from the normal pulp.

Although the series of animals in which the artery alone was divided was five in number, in only two was the inferior dental nerve preserved; these, however, were of considerable interest. In cat 13 the artery was divided fifteen days before the animal was killed, and in cat 9 twenty-nine days. In the nerve from the operated side of cat 13 many of the axon cylinders were markedly changed, some were shrunken, others swollen, while some appeared to have disappeared completely. There was, however, no positive re-action to Marchi and the myelinated sheath seemed normal. This result supports the conclusions of Euler that the nerve is markedly affected by ligature of the artery. In cat 9 this was not the case, for the nerve on the affected side showed no alteration in its axon cylinders. Several explanations might account for the variations obtained in the two experiments.

1. The anastomotic channels in the blood vessels in cat 9 had longer time to open out, and this might have enabled the nerve to recover. Judging by the marked changes which had taken place in cat 13 it does not seem probable that such a recovery could have occurred so rapidly.

2. The nerve at different points in its course may receive its blood supply from different arteries. As no special precautions were taken to obtain absolutely corresponding sections, this explanation might account for the results which were obtained.

3. The blood supply to the nerve may be subject to variations in one individual as compared to the other and cat 9 might have been a case where the anastomotic channels were very numerous, and thus have prevented any changes taking place in the nerve.

At the moment I am inclined to believe that the second explanation is the most probable one, but in order to clear up the problem a further series of experiments is being made.

We will now consider the results which were obtained in those animals which had both the artery and the nerve divided. The technique for the preparation of the sections has been outlined above, and it only remains to be added that precautions were taken, as in the first series of experiments described in my former paper, to see that the nerve had undergone degeneration. This was done by treating the nerves from both sides of the jaw with Marchi's stain, when all the divided nerves were found to have degenerated. There is no analogous method by which the division of the arteries can be checked, but in each case a careful post-mortem examination was made, which showed definitely that the artery and nerve had been divided at the operation. In each case a plug of fibrous tissue blocked the inferior dental foramen, and on one

occasion the plug was examined histologically when it was found to consist solely of fibrous tissue, without any sign of the artery or nerve.

This series consisted of three animals; Nos. 7 and 8 were killed twenty-five days after operation, and No. 12 twenty-seven days after operation.

Figs. 3 and 4 are sections from the posterior teeth of cat 8 and illustrate the type of result which was obtained. The section shown in fig. 3 is from the normal side, and in it the fibres of Mummery will be observed passing outwards from the pulp towards the dentine. At this point they terminate quite suddenly, giving the impression that if the dentine were less densely stained, the fibres could be followed into that tissue. It will be seen that the fibres as they pass peripherally must have run between the odontoblast cells, which in this section, as is very frequently the case, have not stained with the Beckwith method. If fig. 4, from the side of the operation, be now examined, it will be seen that in this section the fibres of Mummery are just as conspicuous and quite as numerous as in fig. 3, and this despite the fact that the whole of the nerve supply to the tooth from the inferior dental nerve and the periarterial plexus has been cut off.

Similar results to those described in the last paragraph were obtained in all three animals in this series of experiments, and thus definitely prove that Mummery's fibres cannot arise from either the nerve or the periarterial plexus. There is a possibility that these two sources are not the only ones from which the pulps of the teeth (in the mandible) obtain their nerve supply. Some dentinal twigs might run with other branches of the trigeminal nerve, as for example the long buccal, or might even come by some entirely different course. Although we have not yet been able to establish this hypothesis, certain unpublished results which Mr S. L. Wilson and myself have obtained during an investigation into the results of regional anaesthesia do suggest that some such extra source of supply is quite a possibility. However, such nerve fibres must necessarily be relatively very few compared to those coming by the normal course. If the latter source of supply is cut off as was done in these experiments, and the fibres of Mummery were the terminal fibres of all the nerves, by far the greater number ought to have disappeared, leaving only a few associated with nerves other than the inferior dental nerve and the periarterial plexus. We have already seen that this is not the case, for the fibres of Mummery did not diminish in number after operation. We have therefore to come to the conclusion that the fibres of Mummery are not of nervous origin and therefore can have nothing to do with the innervation of the dentine.

As to what they really are, there is at present no definite evidence. Professor Hopewell-Smith considers that they may be the same as the fibres of von Korff. In my last paper I came to the conclusion that this view was doubtful, and I am still forced to adopt the same attitude, for although they occupy the same position and have a similar appearance to von Korff's fibres, my difficulty up to the present has been that using his methods I have been completely unsuccessful in obtaining the structures which he describes. Until

this has been done it is impossible to compare the two types of fibres. For the present the nature of Mummery's fibres must remain doubtful.

There has been recently one important contribution to our knowledge of the innervation of the dentine by Tojoda. Unfortunately it has not been possible to obtain a full account of his work, and therefore it has been necessary to rely entirely upon two summaries, one by himself(3), and another in the *British Dental Journal*(4). It appears that Tojoda had been investigating the innervation with metallic impregnation methods, and obtained results similar to those of Mummery. Like Mummery and myself he found it extremely difficult to trace these fibres farther than the edge of the dentine, although from their appearance one would expect them to pass on into that tissue.

Tojoda put this down to the dense formation of precipitation of the metals in the dentine, which prevented any details of its structure being seen, and therefore made it impossible to trace the fibres to their destination. He considered that the intense precipitation in the dentine was due to small amounts of acid and calcium salts, which it was impossible to remove even by prolonged washing with distilled water. To get rid of these substances Tojoda passed an electric current through a tube containing water, in which the specimen was placed. By this means he claims to have driven out all the waste products from the dentine. He then stained the preparation with Bielschowski's stain (bulk method) and after making histological sections was able to trace the fibres into the dentinal tubes for a considerable distance "where they accompany and lie upon the dentinal fibrils. In the tubules they branch and send out shoots which end at times in oval thickenings" (*B.D.J.* summary). On account of the fact that they stained with Bielschowski's method, he concluded that they must be nerve fibres.

I have not yet had an opportunity of trying Tojoda's electrolytic method, but if it removes the waste products, as he claims, it will be of considerable assistance in the investigation of the contents of both teeth and bone. In regard to his conclusion that the fibres are nerves, there is at least one criticism. We have seen that Tojoda relies upon the fact that Bielschowski's method stains these fibres for his proof that the structures in question are nerves. It is, however, well known that in specimens containing a large amount of connective tissue, this technique is very unreliable, as are most of the impregnation methods. There is a great liability of connective tissue fibres being impregnated just as effectively as the nerve fibres. Tojoda is therefore not justified in coming to the conclusion that the fibres which he has found are nerve fibres. To establish such an hypothesis, he must confirm his results, by following some such course as that described in this paper. If after section of the nerve the fibres are found to have disappeared, he will have established his hypothesis, and will have demonstrated conclusively not only that the dentine is innervated, but the nature of its innervation. If the fibres do not disappear, then clearly they are not nerves, and it will have to be concluded that Tojoda has merely again found those structures which histologically look like nerves.

SUMMARY AND CONCLUSIONS

This paper contains an account of a further investigation, by means of the experimental method, into the nature of the fibres of Mummery.

The effects of division of the artery of supply to the teeth upon the dentinal pulps has also been enquired into.

In the latter part of the paper the investigations of Tojoda into the innervation of dentine are discussed.

It is shown that:

1. Ligature of the inferior dental artery causes little alteration in the pulp tissues. This confirms Euler's work.

2. The fibres of Mummery are still present after the trigeminal and sympathetic nerve supplies to the teeth are cut off. It is therefore concluded that Mummery's fibres are not nerves.

3. The work of Tojoda requires confirmation by the experimental method.

The expenses of this investigation have been met by a research grant from the University of Manchester. I have again to express my thanks to Professor Stopford for allowing me to carry out this research in his department, and to Professor Raper for permission to do the experimental work in the Physiology Department. Mr H. Gooding has prepared the micro-photographs, and my wife has again given me great assistance in preparing this paper for the press.

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(2) Stewart, D. *Journ. Anat.* vol. lxi, pp. 439–451, 1927.
(3) Tojoda. *Shikwashimpo*, vol. xx, 1927.
(4) —— *British Dental Journal*, vol. xlix, 1927.

INDEX OF ABBREVIATIONS

D = dentine.	*O* = odontoblasts.
P = pulp tissue.	*F.M.* = fibres of Mummery.

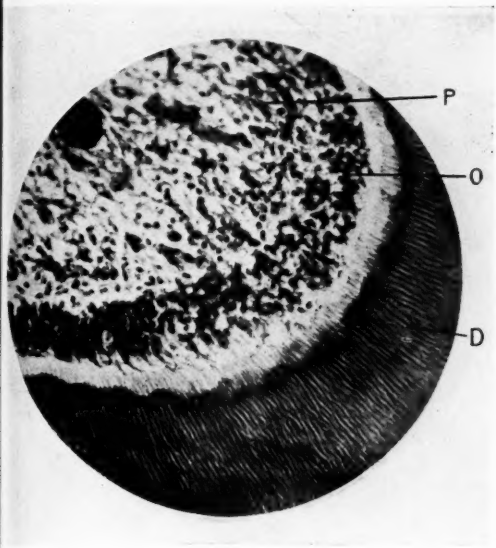
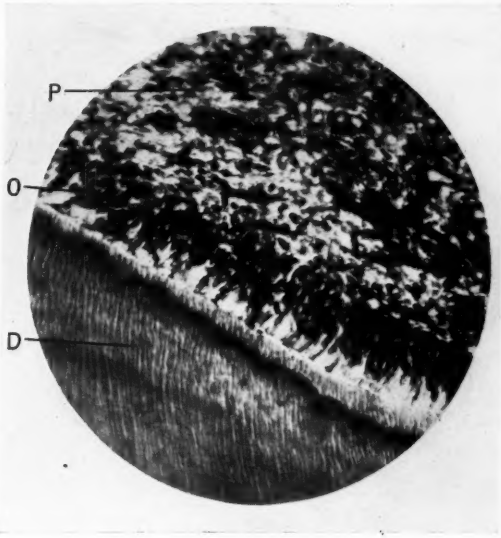


Fig. 1.



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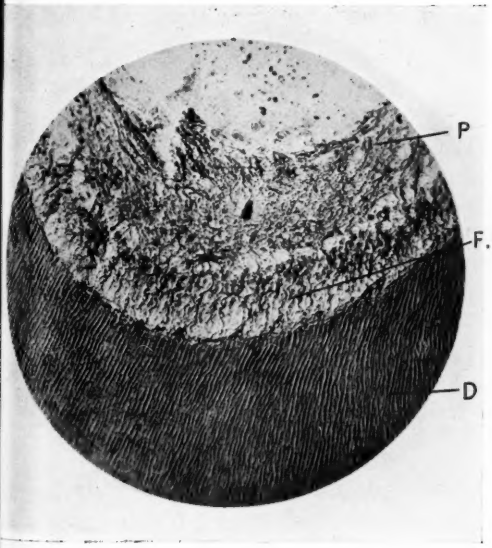

Fig. 3.

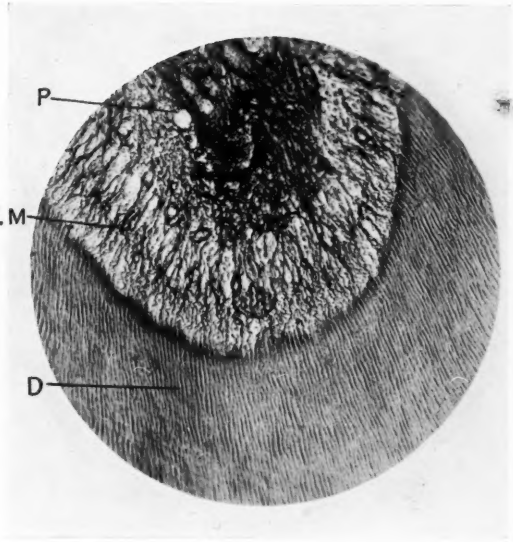

Fig. 4.

DEVELOPMENT OF THE REGION OF THE ISTHMUS RHOMBENCEPHALI

J. ERNEST FRAZER, F.R.C.S.
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It does not appear that much attention has been paid to the ontogenetic development of the region of the isthmus rhombencephali, in spite of the interest attaching to it from many points of view. Some years ago I was struck by the appearance of invagination of the hind-brain in this part, when I was making observations on relative positions of the fourth nerve, and I have recently confirmed and extended these earlier findings. The interest and importance which might be connected with them seem to justify their production in this paper, and it will simplify the matter if the nerve and some of the problems associated with it are considered first.

(*a*) THE EMBRYONIC ISTHMUS AND THE FOURTH NERVE

In Plate I are shown drawings, from models, of the region in embryos of 12, 16, 21, and 26 mm.; these are seen in sagittal section, and in the cases of the 12 and 16 mm. specimens a view is also given of the cranial slope of the hind-brain in each. Looking at this cranial slope one is struck by the fact that alar and basal laminae are prolonged upwards and forwards above the opening into the mid-brain. In the 12 mm. embryo the laminae, although evident, are not very sharply defined, but in the older one they are very clearly cut, the upper part of the alar lamina on each side showing already the beginning of its slow cerebellar change. Turning now to the sagittal section of the 12 mm. embryo, the basal lamina is seen passing up beside the passage into the mid-brain, forming its lateral boundary, to reach the upper part of the hind-brain above this. The mid-brain shows a thick "floor lamina," above which the thin side wall of the large cavity is made by the tectum. The floor lamina is continued in a backward and downward direction into the basal lamina of the hind-brain at the lower part of the side wall of the opening between the two brain regions, and in doing this meets the basal lamina at an acute angle, opening upwards and forwards: the deep sulcus made in this way between the two laminae, and running into the angle, can be referred to for the purposes of this paper as the *intralaminar sulcus*, this name covering its present appearance and its later fate.

By the 16 mm. stage the basal lamina has evidently grown in thickness, leading, with its fellow, to more marked narrowing of the mid-brain opening, and the sagittal section shows that, in its growth, it bulges to some extent into the mid-brain. In doing this it is applied to the upper surface of the floor lamina, making a longer and well-marked intralaminar sulcus, the terminal angle of which is moved a little forward. There is a definite forward movement of this part of the hind-brain with reference to the dorsal notch which marks the isthmus, for the dorsal decussation of the fourth nerve is on the hind-brain in the 12 mm. embryo, but has moved forward in the later specimen, in which it occupies the angle of the notch (see Plate I, fig. 1). It is possible, perhaps probable, that some of this change in position may be due to the backward push of the growing mid-brain tectum, but this, judging from the condition of the tectum in the neighbourhood of the lamina, cannot be considered to be a factor of much importance, whereas a forward growth of the hind-brain structure is only in keeping with the undoubted nature of the process as seen in subsequent stages.

This displacement of the nerve from an original situation in the hind-brain seems to be fairly constant—so far, at least, as my own observations extend on other forms. In the human embryo the decussation is always in the hind-brain up to the stage of 15 or 16 mm., its position in the earlier stages being rather further back than shown in the embryo of 12 mm. This may perhaps explain the statement, occasionally made, that the nerve appears later than the other cranial nerves: it seems to me that it may be found as soon as the other cranial nerves, although it must be admitted that its minute size renders its recognition difficult in young embryos.

The next stage seen in Plate I, that of 21 mm., shows the appearance of a new factor in the modelling of the region. The alar lamina now presents the appearance of being carried forward into the mid-brain, lying above the original basal projection, which is thus pressed down against the floor lamina. The intralaminar sulcus, as a result of this, undergoes a fusion of its opposed walls, the fusion progressing from behind forward, so that on surface view the deep sulcus is now represented by a shallower groove leading to the angular open region. Behind and above this angle is the dislocated basal lamina, and the displaced alar structure above and behind this again. Sections show the fused walls of the intralaminar sulcus as a thick shelf of darkly staining ependymal nuclei projecting into the laminar structure for a considerable distance.

The last specimen drawn, one of 26 mm., shows a little advance; the basal and floor laminae are more closely united, with a less marked groove between them, the alar portion is perhaps more evident, and some new structures associated with the tectal growth are beginning to come into view above these alar and basal parts. It is to be noted that the nerve decussates still at the bottom of the dorsal angle. This is really its definitive position (to which it may therefore be said to attain at 16 mm.) and it is not affected by the appearance of the alar lamina here: the explanation of this will come later, but it may be

said here that the appearances, as seen from within, are in a sense a little deceptive so far as the alar lamina is concerned.

It remains to call attention to the recess in the middle line of the floor, below the junction of floor and basal laminae. The interpeduncular ganglion is formed from the thick ependyma at the angle of this depression, which makes it useful as a topical point, and the recess may be referred to when necessary as the *interpeduncular recess.*

The developmental stage reached so far has, for all practical purposes, put the nerve in its final position. Its decussation has been shifted forward to the hinder limit of the mid-brain, and its nucleus of origin has been carried into this region of the brain by the dislocation forward of the basal lamina. At 12 mm. the nucleus[1] is in the front part of the basal lamina, about halfway up the height of the side wall of the mid-brain opening. As this lamina is carried forward and downward against the floor lamina, the nucleus is carried in the same direction, and the original front face of the basal lamina being now the upper wall of the intralaminar sulcus, the nucleus is now in contact with this. As the walls of the sulcus disappear the nucleus is no longer held back by it, and there is some reason to think that it is displaced further downwards and inwards at more advanced stages as a result of pressure from other formations. There would seem to be in these changes a very simple explanation of the angled intracerebral course pursued by the nerve.

There are two problems of greater interest, however, connected with this nerve, which up to the present have not received any adequate explanation—its dorsal exit and its decussation after its origin.

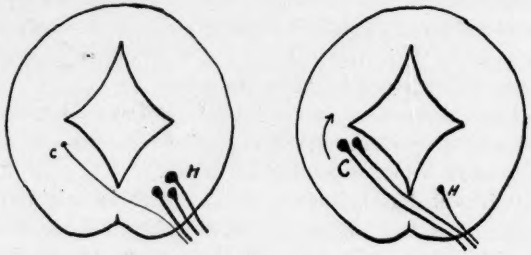
In dealing with the dorsal situation of the superficial origin of the nerve, it is necessary to refer to that part of the hind-brain which has been seen to be above the opening into the mid-brain. In this part are two laminae, basal and alar, on each side, directly and evidently continuous with the same undoubted structures below the level of the opening. Examination of sections shows that the structure of the upper parts, the disposition of neuroblast nuclei, etc., are exactly as in the lower portions, and there does not, in fact, seem to be any reason at all for regarding them as anything other than the continuations of these parts. In other words, the floor of the hind-brain is continued past the opening into the mid-brain, as is really at once evident on looking at the examples in Plate I. Comparing this aspect with the embryonic structure of the spinal cord, as a standard, it would seem better to restrict the term "floor" to the basal laminae, for it is customary to consider the cord to be "roofed" by the dorsal laminae and the roof-plate joining them.

The basal laminae, then, of the upper part of the hind-brain, above the level of the mid-brain opening, make a true floor to the neural tube here, and the thin layer joining them across the middle line is evidently an ordinary

[1] Of course only an approximate position can be given for the "nucleus," the ependymal thickening around the apparent termination of the nerve fibres being taken for this purpose.

floor-plate: they form here the ventral moiety of the neural tube, just as they do lower down, and in the spinal cord. Hence the fourth nerve, when it first appears, makes its exit from the ventral surface of the tube, as is the case with all efferent roots. This ventral surface is then moved toward the mid-brain, to the isthmus. As the original situation was above the mid-brain, it follows that the ventral surface when it moves must reach the dorsal aspect of the isthmus, just as it would reach the ventral aspect if it moved from below the level of the opening. The attainment of the isthmus, then, is the result of the forward move, and the dorsal position here is the necessary registration or expression of the originally ventral situation of the nerve. The nerve is essentially ventral although actually dorsal.

But although we can refer the dorsal origin in this way to the existence of an upper portion of the hind-brain, from which the nerve originally arises, no light is thrown on the meaning of the presence of such a part of the brain. I have not so far been fortunate enough to meet with any adequate suggestion in developmental occurrences, and must perforce be content to leave the matter there for the present.



Text-fig. 1. Schemes to show the essentially similar nature of a dorsal efferent root and of the fourth nerve (right). *C.*, *H.* contralateral and homolateral origins. The arrow indicates that the contralateral origin of the fourth nerve is secondarily displaced further away, as is mentioned in the text.

The question of the meaning of the decussation after origin does not admit of solution on mechanical lines similar to the previous one, but there is, I think, good reason for saying that it may be explained on general grounds connected with the origin of many, if not all, efferent roots. It is known that the anterior roots of the spinal nerves, in addition to the fibres derived from ventral horn cells of their own side, possess also fibres which arise from cells situated on the other side of the cord. These contralateral fibres cross in the white ventral commissure and pass from there directly into the issuing root. The cells giving origin to them are described by Winkler as being in what he terms the "pars intermedia" of the cord, and the fibres are destined for the "sympathetic" system. Presumably, also, there is some cerebellar influence exercised on these cells, for Winkler describes cerebello-fugal fibres as reaching this same zone. We may say, then, that (in the dorsal, dorso-lumbar, and probably sacral

regions at any rate) the spinal efferent roots have homolateral and contralateral origins: this is shown in the left-hand diagram in text-fig. 1, where *C* is the relatively small contralateral element in the root, and *H* the large and overshadowing homolateral portion. The condition which, it seemed to me, might be represented by the fourth nerve is shown on the right side, where the homolateral element is reduced to a minimum, while the contralateral portion is forming practically the whole of the nerve. This puts this nerve quite in line with the other, only differing in the proportions existing between its constituent parts, while its contralateral fibres cross in the ventral commissure, which is of course superficial here owing to the absence of the ventral projections which are so marked in the spinal cord. Taking this idea as a working hypothesis, a search was made for some representative of the homolateral origin, if perchance it might still be in evidence, and I think I have been able to find such a remnant: this has so far only been found in the older specimens, the younger ones being indeterminate in all their nuclear structures, as already pointed out. The small bundle of fibres to which I refer has been found in all stages examined, after the middle of the third month and up to the time of birth (see Plate III, *C*). The cells from which they seem to arise form a group about halfway down the side wall of the cavity, in what would, probably, have been the upper part of the (now invaginated) basal lamina. My sections, however, are ordinary serial sections, stained in the ordinary routine way, and I cannot be quite certain that the bundle actually arises in this way, although I believe that the observation is correct. Under these circumstances I was glad to find and fall back upon the experimental results of van Gehuchten, who described, in the rabbit, the existence of homolateral degeneration occurring after destruction of the fourth nerve. This was an example of secondary degeneration, some weeks after the ablation of the nerve, and the result seems to have been quite clear.

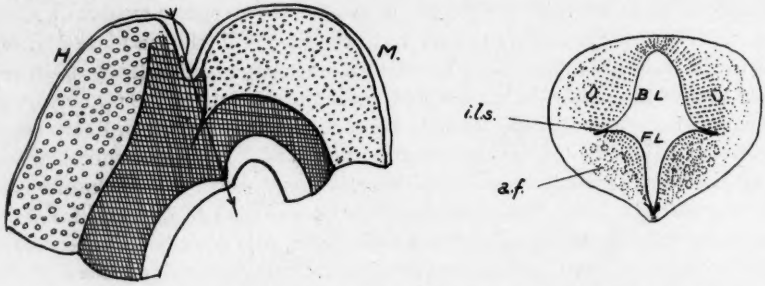
The explanation offered, then, for the problem of the decussation is little more than a suggestion, having value only in so far as van Gehuchten's experiment and the observations on the human embryo may be considered to have weight. The suggestion, simply, is that the nerve is like other efferent roots, possessing homolateral and contralateral origins, but differs from them in that its contralateral part completely overshadows the other, so that practically the whole nerve decussates.

Sagittal sections of the region in embryos of 35 mm. and 48 mm. are shown in Plate II, fig. 1. They exhibit progressive changes on the lines already indicated. The intralaminar groove has disappeared completely, and the interlaminar sulcus is very deep. The tectal thickening is progressing slowly, and two rounded masses, already faintly indicated in the 26 mm. stage, are now seen to be advancing inwards in the floor of the caudal projection of the midbrain, above the region occupied by the basal lamina.

(*b*) THE DEEPER STRUCTURE OF THE REGION

The method of transverse section can be taken as a convenient way of illustrating the changes taking place during the building up of the region of the isthmus. The line of section which has been adopted passes through the dorsal notch above and the interpeduncular recess or ganglion below, these being easily defined: thus the sections (reconstructed) are approximately similar and comparable.

The first figure in text-fig. 2 is a diagram intended to show the disposition of the several parts entering into the formation of the wall of the cavity in the 12 mm. embryo. In the hind-brain (*H*) the basal and alar areas are represented respectively by cross-hatching and small circles, while the tectal region of the mid-brain (*M*) is shown by dots. The floor lamina of the mid-brain is marked like the basal lamina, with which it is continuous. It must be noted here that



Text-fig. 2. On the left, a scheme showing the component parts in the regions of hind-brain, *H.*, and mid-brain, *M.* Further explanation in text. The arrow gives direction of section (on right). *BL.* basal lamina, *FL.* floor lamina, *i.l.s.* intralaminar sulcus, *a.f.* area of short association fibres.

this floor lamina contains a well-developed zone of short association fibres lying against its thick ependymal layer, extending back to the basal lamina and forward to the region of the third nerve nucleus.

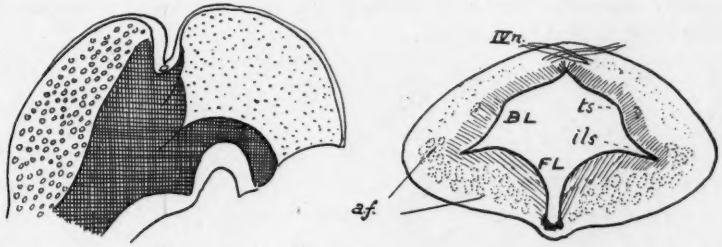
These fibres, although best marked in this stage in the mid-brain, are at any rate indicated to some degree in the hind-brain. Later, as will be mentioned, they extend, and it becomes evident that they are the primary foundation of the posterior longitudinal bundle. They do not reach the region of the posterior commissure at the 12 mm. stage, nor for some little time after this. The fibres in the commissure are forming, however, but are quite distinct from those now being described. I hope to be able to enter more fully into these matters in a future communication.

The transverse section (text-fig. 2) thus shows a lower part, the floor lamina, marked by the association fibres and separated above from the upper part by a deep cleft, which is the intralaminar sulcus. The part above this sulcus is the basal lamina, containing no association fibres. The trochlear nerve, issuing from the hind-brain at this stage, is not cut at the top of the

section, but is divided lower down near its nucleus, which is just in front of the line of section. Thus there are nothing but basal and floor structures in the section of the isthmus region, and the thickness of the floor lamina seems to be due almost entirely to the large formation of association fibres.

Coming to the 16 mm. stage, there is decided growth of the basal lamina, and also to some extent of the floor lamina. The association fibres have increased considerably, and are now definitely continued into the hind-brain. In addition they are involving the portion of the basal lamina which is laid against the floor lamina, turning round the hinder and shallower part of the intralaminar sulcus in doing so.

The section shows (text-fig. 3) the early result of the growth of the basal lamina. The intralaminar sulcus is being pushed down in the side wall and is being invaded by the groups of association fibres. The nerve is now cut in decussation in the roof.



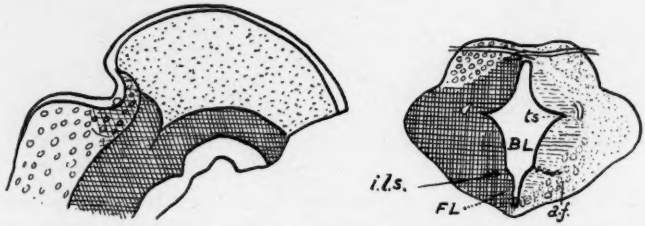
Text-fig. 3. 16 mm. stage. Position of structures, indicated as in last figure. Section through isthmus: fourth nerve decussating in roof, *t.s.* translaminar groove, other references as before.

The section at this stage, then, shows considerable modification in the form of the cavity, with lowering and closing of the intralaminar sulcus and the beginning of a new secondary "translaminar" groove higher up, dividing the basal lamina into upper and lower parts. The whole wall, however, is still composed only of basal tissues, in which the nerve decussates in the roof and an increased area of association fibres lies in the lower part.

The 21 mm. stage is of interest, because in it the dorsal lamina appears to have reached, essentially if not actually, the small degree of forward movement as a whole which seems to have been necessary to admit of further extension of its parts.

Two sections are shown in Plate II, fig. 2, on the right through the hind-brain of an embryo of 19 mm., just below the interpeduncular angle, on the left through an embryo of 26 mm. at a lower level. The neuroblastic groups are shown as shaded areas. It is not necessary to go into the matter of their derivations in this paper, and the sections are introduced to show the low prominence *a* on the outer surface of the hind-brain, more or less opposite the

junction of alar and basal laminae. This is only the sectional appearance of a ridge running up this part of the hind-brain, evidently caused by a condensation or collection of neuroblasts in this situation. The ridge is visible, though ill-defined, in the 16 mm. specimen (Plate II, fig. 3) and passes, of course, up towards and on to the upper part of the hind-brain, above the level of the isthmus. In the 21 mm. embryo (on the right in Plate II, fig. 3) the growth of the alar lamina has moved the ridge forward, so that its front part reaches and runs on to the caudal end of the mid-brain, beyond the dorsal notch of the isthmus: in the figure the projecting part of the mid-brain is represented as raised up, to give a better view of the upper end of the ridge. The important thing connected with this ridge is that—when they are first found—the fibres of Gowers' tract lie in the clear zone behind the neuroblastic condensation, while those belonging to other tracts and reaching the mid-brain ultimately are placed in the clear areas in front of it: these latter areas, then, as the result of the changes reached in the 21 mm. embryo, are brought into relation and continuity with the mid-brain, whereas the spino-cerebellar fibres are left further back, behind the isthmus.

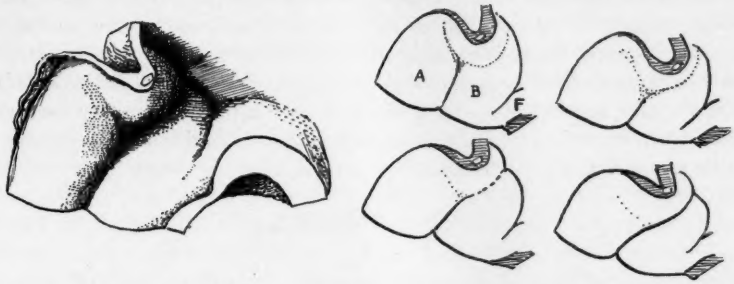


Text-fig. 4. Schematic analysis of 21 mm. stage (left), with section through isthmus (right).

The growth of the alar lamina, which has led to the changes on the outer aspect which have just been considered, has its effect also on the internal appearance, as has been shown in Plate I. As already mentioned, however, this appearance is deceptive. The schematic analysis of the part is given in text-fig. 4, where it can be seen that the alar region, although carried forward and separated by what is apparently an interlaminar sulcus from the (lower part of the) basal lamina, is occupying here a situation in which the marking of the basal structure is still represented. The explanation is that the basal lamina remains, and alone forms the side wall of the cavity here, while the derivatives of the alar lamina, in growing forward, pass on its outer side. The appearance of an interlaminar sulcus is produced by a modification of a condition faintly foreshadowed in the 16 mm. embryo.

In this embryo (Plate I) it can be seen that the upper part of the basal lamina, for a little distance below the nerve, projects somewhat into the cavity. This can be seen also on section (text-fig. 3) where the upper projection is separated from the rest of the basal lamina by a shallow depression: this has

already been noticed as a "translaminar" groove, crossing the basal lamina (Plate I) in a U-shaped manner. The hinder limb of the U-groove is lost in the upper part of the true interlaminar sulcus. When the alar lamina begins to grow in thickness the interlaminar sulcus is pushed forward, so that it runs into the U-groove nearer its lowest part. This is seen in text-fig. 5, in which a sagittal section of the region in an embryo of 19 mm. is shown[1]. The other



Text-fig. 5. Sagittal section, 19 mm., on left, showing the intermediate stage in the changing aspect of the wall of the cavity. On the right, schemes to represent the method in which the change is brought about. *A*, *B*, *F*, alar, basal, and floor laminae.

diagrams in the figure show schematically how the change is effected: the forward displacement of the interlaminar sulcus makes a groove system of a Y-shape, and there is a rapid deepening of the front limb of the Y, with an equally rapid shallowing and practical disappearance of the hinder limb, whence it comes about that the stem and front limb remain as a continuous sulcus. It is evident, however, that although the groove made in this way has all the appearance of an interlaminar sulcus, its upper and front part, in the region of the isthmus, is actually translaminar.

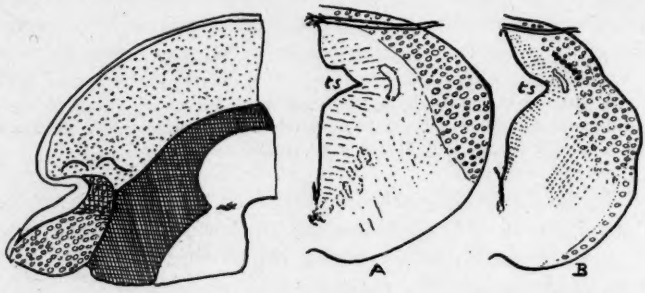
In this way, then, the section across the isthmus (text-fig. 4) of the 21 mm. specimen shows the basal lamina lining the cavity, with the deep translaminar sulcus cutting into it, while a small ependymal thickening, low down, marks all that is left of the originally deep intralaminar groove. The association fibres (or posterior longitudinal bundle, as one might now venture to term the collection) extend now well above the intralaminar remnant, and the lamina is thickening outside this, with a scattered mantle layer of nuclei. The alar lamina is now represented by a small area of the section outside and above the translaminar sulcus. This addition to the section has included the issuing nerve in part, burying it in its course to a small extent.

Text-fig. 6 gives the schematic analysis of the 35 mm. stage, with a half-section (*A*). It can be seen that the basal wall of the cavity is practically as before, save that there is now no sign of the intralaminar remnant, the

[1] An embryo of 18 mm. provided comparable results. As many of the sections however had been injured, I was very glad to have the opportunity of examining this perfect specimen, for the loan of which I am much indebted to Dr R. Gladstone.

trans-laminar being represented alone as a deep groove. The lower part of the basal area has thickened considerably, with migration of neuroblasts. The main feature, however, is the great increase in size of the alar area, which now extends down well over the outer part of the basal formation.

The second half-section, *B*, represents the conditions in the 48 mm. specimen, at a much smaller magnification. The alar growth is now larger and a ventro-lateral extension of it is shown: whether this is really alar in formation, or a secondary involvement of the basal surface by fibres running to the alar structures, cannot be decided, although the latter seems to me to be the more likely explanation. Fibres extending (superior peduncle) into the basal region from the alar, are clearly seen: these, as a matter of fact, are also suggested to some extent in the 35 mm. embryo. The ventro-lateral fibres seem to belong to the lateral lemniscus formation.



Text-fig. 6. Schematic analysis, 35 mm., on left. Sections *A* 35 mm., *B* 48 mm.

A more interesting set of fibres, however, is found in this specimen, which could not be picked up with any certainty in the earlier embryo. Plate III, fig. 1, *A*, is a section running through the roof of the fourth ventricle dorsally, a little distance behind the isthmus, while its oblique direction carries it ventrally through the group of nuclei connected with the fifth nerve. Certain fibres are clearly seen extending between these dorsal and ventral regions which are assumed to be connected with the nuclei and nerve. It is impossible, of course, to assert positively that they are so connected, but, to my mind at any rate, there can be little doubt about the matter, and the ultimate distribution of the fibres, when traced cranially, seems to decide it. At the level of the section the fibres can be seen to reach small nuclear masses in the ventricular roof, and also, by the inner fibres, to be connected with large cells or small cell groups near the interlaminar sulcus. As they are followed upwards in successive sections the fibres going to the interlaminar region seem at first to be associated more with cells on the basal side of the groove than with alar cells, but there soon comes a change: the fibres now pass round the groove and reach cell groups on its alar side. Then these groups leave their near relation to the ependyma and become relatively deep, and in this way the isthmus is reached.

The position of the groups or cells is now shown in the section (text-fig. 6) by large black dots This clearly represents the mesencephalic root of the nerve, and it extends forward at this stage only as far as the alar invasion seems to have extended, that is, to the deep hollow in front of the invaginated parts.

The level at which the cells associated with these fibres sink to a deeper situation seems to correspond with the passage of the true interlaminar sulcus into its translaminar portion, in other words with the forward growth of the alar lamina outside the basal structure. It is of much interest to observe that this extension of the connections of the fifth nerve into the mid-brain is associated with the alar lamina. I have made no observations on its further extension forward.

Models of the region in embryos of 75 mm. and 100 mm. show no essential difference in the region of the isthmus. The cavity seems smaller, partly owing to the relative size of the surrounding parts, but also perhaps because it is actually smaller. The translaminar sulcus is very deep, the wall above it being flattened down. Otherwise, the cavity is the same as in the earlier stage, and the solid structures outside it are further differentiations *in situ* of the parts placed in position in this earlier stage. This general description seems to be applicable to the conditions throughout the rest of foetal life, and the state in the fifth month (Plate III, *B*) illustrates this very well. The next figure (*C*) gives an illustration of the homolateral origin of the fourth nerve, such as may be found, apparently, in most specimens in the foetal stages.

Little or nothing would be gained by further description or discussion of what has been brought forward in this paper. I venture to think that the various changes which have been shown, and can be grouped together as associated with the process of "dislocation" in the region of the isthmus, must be looked on as facts, whatever explanation of their occurrence may be adopted ultimately. The same, perhaps, may be said for the change in position of the nerve-decussation in its relation to the explanation of the dorsal exit of the fourth nerve. The explanation of the decussation after origin has been put forward in the form of a suggestion based on comparison with other origins, and fortified by experimental result and observation: it seems to me, I confess, to be in keeping with what is known about the nerve. So far as the other observations are concerned, it must be remembered that they were carried out on ordinary serial sections not made with any special object nor stained in any special way: as a rule iron haematoxylin was the stain used, occasionally counterstained with eosin. Under these circumstances I imagine that the observations err on the minimal side, that is, for instance, the fibres described were probably there at an earlier stage than that in which one could certainly recognise them, and their field of extent was possibly larger than it seemed to be, and so on. These, after all, are faults on the right side, if they exist, so no more need be said about them. Beyond indicating its position and extent, nothing has been said about the tectal growth in the mid-brain, because it is not really concerned in building up the region of the isthmus. In the later

stages figured, the slow ingrowths of this formation are to be seen above those described, and it is only necessary here to add that this slow growth leads gradually to the closure of that portion of the cavity contained in the projection of the mid-brain caudally: the cavity is closed in a specimen of 115 mm.

SUMMARY

1. The floor of the cranial slope of the hind-brain is continued upwards past the opening into the mid-brain.

2. The fourth nerve has its superficial origin at first from this upward prolongation of the floor.

3. The basal lamina beside the mid-brain opening is displaced forward into this, and folded down against the floor lamina of the mid-brain, producing an intralaminar sulcus. Thus the nucleus of origin of the fourth nerve is carried forward and put in immediate relation with the intralaminar sulcus.

4. At the same time, with the forward displacement of the upper part of the basal lamina, the decussation of the nerve is carried on to the dorsal surface of the isthmus. This dorsal position is therefore only the necessary result of the displacement of the original ventral origin on that part of the hind-brain above the region of the isthmus.

5. The alar lamina is displaced forward, passing on the outer side of the basal lamina in the isthmus, and thus leaving this lamina to form the wall of the cavity here. The displacement of the alar lamina enables formations associated with it to reach the mid-brain.

6. A deceptive appearance of an interlaminar sulcus is produced in the region of the isthmus by the deepening of a translaminar groove across the basal lamina. The intralaminar sulcus disappears by fusion and breaking up of its ependymal walls, after it has been pushed down to a low level in the wall of the isthmus, and the fourth nucleus is thus left low down in the wall.

7. The translaminar sulcus remains as a deep sulcus running through the isthmus, on each side, but the wall, both above and below it, is only made by basal lamina.

8. A short description is given of the general structure of the walls of the isthmus at different stages, the mesencephalic root of the fifth nerve being shown to belong to the alar lamina here.

9. A suggestion is made that the decussation after origin of the fourth nerve is comparable with the decussation of contralateral fibres of origin of spinal nerves: in these the homolateral origin obscures the contralateral, but in the fourth nerve the homolateral origin is reduced to a minimum, and the contralateral becomes the main origin. Some support for this is advanced.

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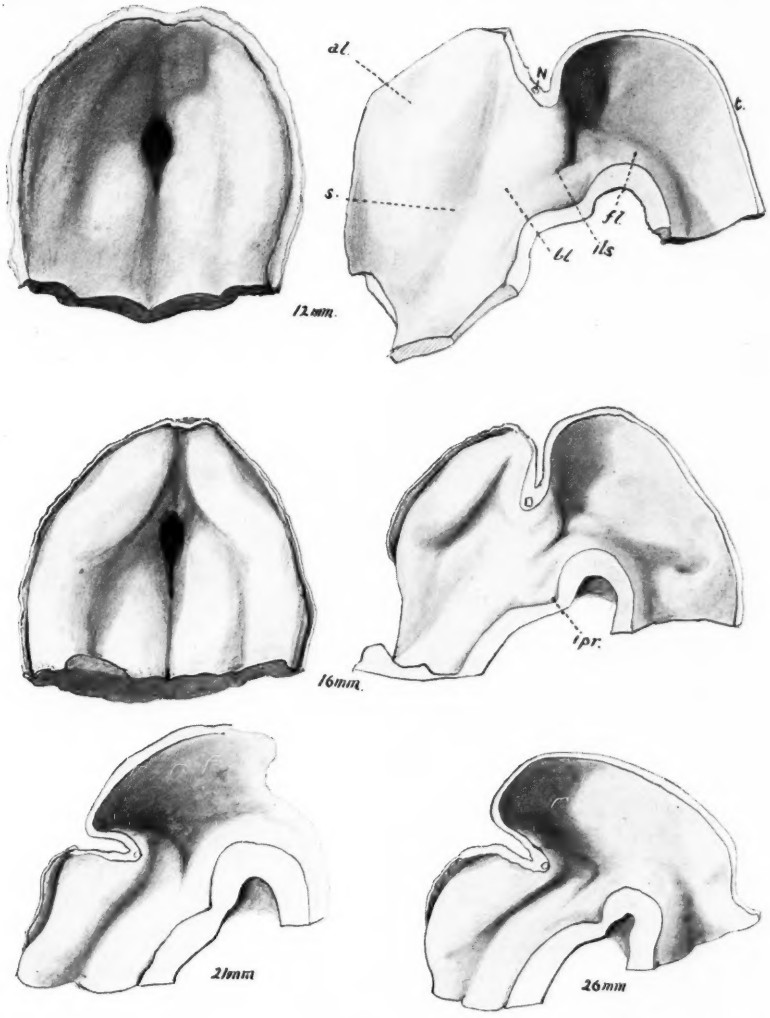

Fig. 1. Above, cranial slope of hind-brain and sagittal section of hind- and mid-brain in 12 mm. embryo. Middle row, similar views of parts in 16 mm. embryo. Lower row, sagittal sections in 21 mm. (left) and 26 mm. (right). *N.* decussation of fourth nerve; *a.l.* alar lamina; *b.l.* basal lamina; *f.l.* floor lamina; *t.* tectum of mid-brain; *s.* interlaminar sulcus; *i.l.s.* intralaminar sulcus; *i.p.r.* interpeduncular recess. Magnifications decrease with advancing age.

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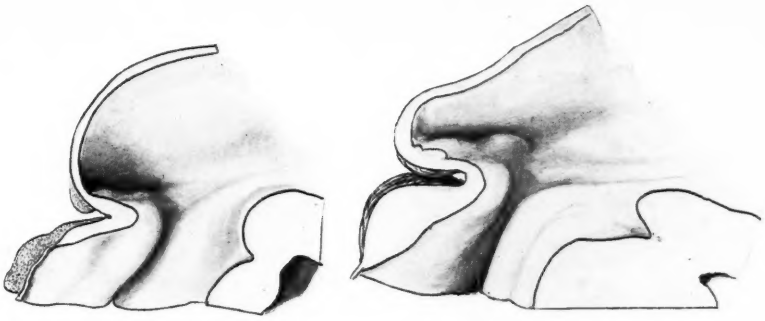

Fig. 1. Sagittal sections through the region in embryos of 35 mm. and 48 mm.

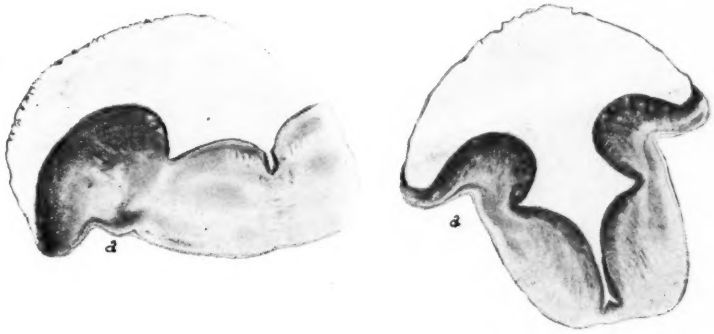

Fig. 2. Two sections through the hind-brain, from embryos of 19 mm. and 26 mm. To show the low ridge, *a*, visible on the outer surface of the hind-brain.

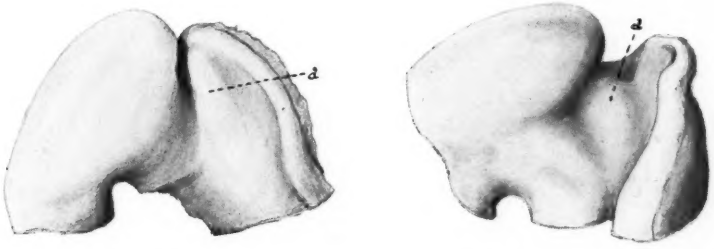

Fig. 3. Outer aspects of the region in embryos of 16 mm. (left) and 21 mm. (right), showing the ridge, *a*. This passes up behind the isthmus in the younger embryo, but runs towards it in the other, so that its front part reaches the mid-brain. The tectum has been raised to show this.

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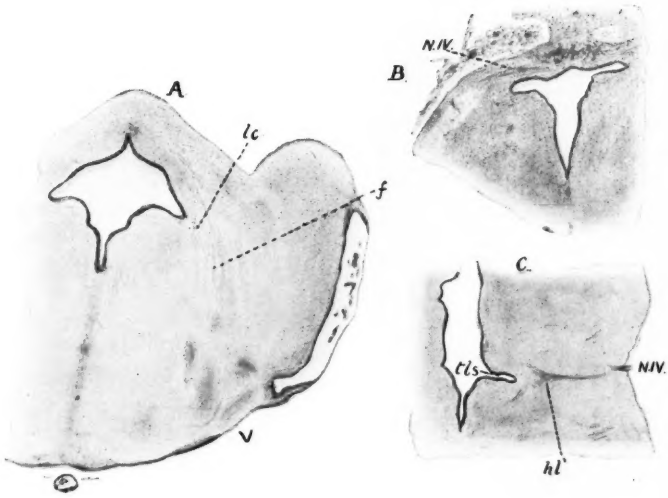

Fig. 1. *A*, section through upper part of fourth ventricle, 48 mm.: *V*, place where fifth nerve appears, immediately above this: nuclear masses associated with the nerve are seen dorsal to this: *f.* fibres extending between the nerve and nuclei ventrally and the roof of the ventricle dorsally, the innermost fibres reaching *l.c.*, which probably represents the locus caeruleus. *B*, section passing in the neighbourhood of the isthmus, 115 mm., to show the flattening down of the root, leaving the translaminar sulcus as the upper limb in a T-shaped cavity. *C*, produced by adding several sections from an embryo of 100 mm., to show *h.l.*, the (?) homolateral roof fibres of the trochlear nerve, joining a separate arched bundle of (contralateral) fibres. The plane of section is very oblique, and runs dorsally into the cavity of the mid-brain; *t.l.s.* translaminar sulcus.

THE FACIAL MUSCLES OF THREE ORANG UTANS AND TWO CERCOPITHECIDAE

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INTRODUCTION

The material for this paper consisted of three young orang utans (*Simia Satyrus*), one young baboon (chacma ape, *Papio porcarius*) and a young *Macacus rhesus* monkey.

None of these Primates was fully grown or aged. The specimens had been acquired at various periods by the Anatomy Department of the University of Sydney, the times ranging from fifteen or more years (Z O 1) to twelve months (Z O 4). All had been injected with a 5 per cent. solution of commercial formalin and kept in casks containing a similar solution. In the older specimens the removal of the skin presented difficulties but the underlying structures were well preserved and were not unduly bleached nor fragile. The baboon Z O 4 had been the leader of a troupe of performing monkeys who had accidentally throttled himself with his chain and thereby added slightly to the difficulties of the dissection owing to the engorged veins. His age was stated to be two years. About the age of the others no data were available. The vertex and buttock measurements would have been misleading as the specimens, whilst freshly prepared, had been placed in a cask, and were in consequence somewhat contorted. Of the orangs Z O 1 was the smallest, being little larger than a well-grown *Macacus rhesus*. In Z O 1 and Z O 2 the skin was pale in colour. Z O 3 was the largest, its skin was shiny and dark in shade, not unlike that of an "aboriginal," but he had not developed as yet the ear-cheek pads. The macaque was a young animal which had been afflicted with paralysis of the legs; a trepanning operation had been performed, and afterwards the brain and spinal cord had been removed by the late Prof. Hunter. Some indication of the age of these Primates may be gained from the number of teeth each possess, and these are shown in the dioptograms of the various skulls (A 8, B 8, etc.). In all cases the left side alone of the head was dissected and the right reserved for the future investigation of the nerve supply. The trachelo-platysma was dissected on both sides of the neck.

When the epidermis had been removed it was found, in the orangs, that no facial muscles were visible, but that they were concealed by a layer of pearly white connective tissue which represented the superficial fascia (panniculus adiposus) of *Homo sapiens*. This fascia split into layers readily and, with the exception of the muzzle (lip region) and neck, contained a very small amount

of fat which was confined to three small areas, viz. a T-shaped area over the upper nasal and medial superciliary areas, the oculo-buccal groove and the temporal region just lateral to the orbit. In this article the fascia will be alluded to as the panniculus incarnosus, as this term could apply equally well to *Homo sapiens*. In the baboon and macaque the fat-laden areas of the panniculus incarnosus were very similar to that just described; the remainder of the panniculus was very thin and delicate and for the most part was removed with the epidermis. In all five Primates the area of the muzzle was covered by dense fibrous tissue mixed with fat, and there was a good supply of fat over the back and front of the neck and over the neck pouches. The panniculus of the muzzle is indicated in most of the dioptograms. When the superficial muscles had been displayed, the head was placed beneath a dioptograph and a careful tracing in pencil made of these muscles. The tracing of the muscles was made by following with a dissecting needle from point to point the various muscle fasciculi; this gave an accurate though rough outline which afterwards was filled in and shaded. The smaller drawings and insets are tracings of the original dioptogram with the extra muscle or muscles drawn in by freehand.

As the dissection proceeded alterations of detail were made where necessary, but the figures represented the true relations of the various muscles before they were disturbed by dissection; they do not possess the artistic merit of a free-hand drawing, but they are tolerably accurate. When the dissection was completed the dioptograms, all of which were life size, were inked in. The awkward attitudes of the subjects not only made the dioptograms difficult to obtain, but it was not found possible always to get a head into the true norma facialis (Frankfort horizontal) position, and even when obtained the true norma facialis did not display well the muscles of the chin; a slightly modified position was adopted for this position, but the norma lateralis was made as accurately as the stiffened tissues would allow. In the dioptograms of the skulls the dotted lines indicate that the bony outline was not able to be traced owing to the intervention of the soft tissues. The dissecting needle indicates the posterior margin of the mental shelf.

More difficult problems were the nomenclature and phylo-genesis of the facial muscles. It was not by intention that this latter question appeared, but by precipitation from the solution of the M. triangularis, and under this head it will be further discussed. The nomenclature adopted for the muscles was the same as for *Homo sapiens*, since the facial muscles found in these Primates did not differ from those found in man more than their respective femurs or radii. To express this otherwise; in these Primates the facial musculature did not differ more from that of the Australian aboriginals than did the facial musculature of these "Abos" differ from that of the European as usually described and figured in the anatomical textbooks.

The overlapping of muscles was certainly greater, and the lines of cleavage were easily overlooked, but such lines of cleavage were definite and well marked. This was noticeable in the M. quadratus labii superioris; after removal

of the epidermis and panniculus incarnosus, the difference in the direction of the fibres of the two capita led to the finding of the line of cleavage, i.e. plane of fine fibrous tissue lying between the two muscles. Contrary to custom the facial muscles have been studied from a functional rather than a neurological standpoint, not because this method was thought to be even equally efficacious, but because the viewing of a subject from a fresh angle often throws into prominence a feature that otherwise would be obscured or overlooked. The grouping and nomenclature of the muscles has been made accordingly, and for this reason the B.N.A. term M. quadratus labii superioris has been retained instead of adopting the morphological classification of H. Virchow. Such grouping is necessarily based upon the experience gained in the cinematograph pictures of the human subject, rather than any direct observations upon lower Primates.

The new terms superficial and deep labial muscles will be understood by reference to the Table of Facial Muscles, and the reasons for the bracketing together of the latter muscles will be discussed under its own appropriate head. Suffice to say here that in the dissection of the orangs the pars perpendicularis of Virchow was suspected to be a labial rather than a nasal muscle. Unfortunately the sections of these lips were accidentally damaged. Carefully prepared sections from a female European fully justified the original suspicion, and photo-micrographs and diagrams of these will be given.

Following each muscle heading a number will be found in brackets; this corresponds to the number given in the list below; which also is used to denote the attachments of the muscle in all the dioptograms of the skulls and modiolar areas.

TABLE OF FACIAL MUSCLES

- 1. M. subcutaneus colli (p. 22)
  - *a.* Noto-platysma
    - 1′. Supra-angularis (Pars aberrans)
    - 2′. Infra-angularis (Pars labialis)
  - *b.* Trachelo-platysma
    - (*a*′) Portio decussata
    - (*b*′) Portio labralis
    - (*c*′) Portio modiolaris
    - (*d*′) Portio mandibularis
  - *c.* Sphincter colli
    - (1′) Superficialis
    - (2′) Profundus
- Mm. labiorum superficiales (p. 37)
  - 2. Inferior (M. quadratus labii inferioris)
  - 3. Superior (M. quadratus labii superioris)
    - (*a*) Caput angulare
    - (*b*) Caput infra-orbitale
    - (*c*) Caput zygomaticum
- Musculi modioli
  - 4. M. zygomaticus (p. 42)
  - 5. M. caninus (p. 42)
  - 6. M. triangularis (p. 44)
    - (*a*) Caput latum
    - (*b*) Caput transversum
    - (*c*) Caput longum
  - 6′. M. buccalis (risorius) (not present)
  - 7. M. buccinator (p. 48)
  - 8. M. orbicularis oris (p. 50)
    - (*a*) Pars marginalis
    - (*b*) Pars peripheralis
    - (*c*) Pars septalis
  - 9. M. incisivi (p. 51)
    - (*a*) Superior
    - (*b*) Inferior

TABLE OF FACIAL MUSCLES (*continued*)

Modiolar Area (p. 53)

- 10. Mm. labiorum profundi (p. 56)
  - (*a*) Superior (Pars perpendicularis M. nasalis (Virchow))
  - (*b*) Inferior (M. mentalis)
- 11. M. nasalis (p. 59)
  - (*a*) Pars transversa
  - (*b*) Pars alaris proprius
- 12. M. orbicularis oculi (p. 60)
  - (*a*) Pars palpebralis
  - (*b*) Pars orbitalis
  - (*c*) Pars peripheralis (M. malaris)
    - (*a'*) Caput mediale
    - (*b'*) Caput laterale
- 13. M. depressor capitis (supercilii) (p. 63)
- 14. M. corrugator (supercilii) (p. 66)
- 15. M. procerus (p. 67)

M. epicranius

- 16. M. orbito-auricularis (p. 68)
  - (*a*) M. frontalis
  - (*b*) M. orbito-temporalis
- 17. M. auriculo-occipitalis (p. 70)
  - (*a*) M. cervico-auriculo-occipitalis
  - (*b*) M. occipitalis
  - (*c*) M. auriculo-occipitalis proprius
- 18. Galea (p. 74)
- 19. M. auriculares extrinseci (p. 75)
  - (*a*) M. auricularis posterior
  - (*b*) M. auricularis superior
  - (*c*) M. auricularis anterior
- 20. M. varii et diversi (p. 76)

M. SUBCUTANEUS COLLI (1)

This comprises four muscles, viz. two platysmae and two sphincters. The superficial sphincter is met with only in Subprimates; in the higher Primates the deep sphincter is seldom seen even as a "Rest" and in the present dissection was not found. Originally this latter was considered as a deep layer of the platysmal sheet (Ruge (41)) but now, though probably both are developed from a common anlage, it is considered a separate muscle. The total platysmal sheet at times is greater than the combined remaining facial muscles, and its size has hampered the understanding of it. The German school first divided this muscle sheet according to its method of origin into a "Nacken-" and a "Hals-" platysma. This was very happy, as it marked an evolutionary distinction as well as one of origin. But the terms used are not of universal application, so it is proposed to call them the noto-platysma (*νῶτον* = back) and trachelo-platysma (*τράχηλος* = the front of the neck), instead of the terms "nape" and "neck" platysma which were used previously. The tip of the acromion process will be regarded as the point where these two muscles meet; Zuckerkandl takes this point also (55).

It is a very small step from the precedent of allowing an independent existence to the sphincter colli to considering as separate muscles these two components of the platysmal sheet. Ruge regarded the trachelo-platysma as an extension of the noto-platysma because it lay in the same morphological plane and was supplied by the seventh cranial nerve; but the origins of the two muscles are different—one being from the front and the other from the back of the neck—and their modes of insertion are different in each species, as the former gradually replaces the latter. Speaking of the platysma in Primates

this author states (*Primaten*, p. 16): "the degeneration of the platysma proceeds from below upwards, so that Gegenbauer was quite right in considering as most constant and independent the upper portion of the muscle which is united to the muscles of the face." That the degeneration of the platysma is centripetal seems correct, but this does not confirm Gegenbauer's statement. The fallacy has arisen from regarding the trachelo-platysma as an extension of the noto-platysma and the whole platysmal sheet as a single muscle, hence not observing the changes taking place in the neck, chin, lips and modiolar area. Had the trachelo-platysma been regarded as a separate muscle newly arrived in the Primates, it would not have escaped notice that at first it is inserted as the portio decussata; little by little it supplants the noto-platysma, first in the chin then in the lips, and modiolar area until it occupies the whole of the strategic pars infra-angularis; finally in *Homo* it ousts the noto-platysma from the pars supra-angularis. This certainly suggests the struggle for existence. Hence it is proposed to regard the trachelo-platysma as a separate though sister muscle to the noto-platysma, probably developing from the same anlage. Little violence will be done to the original concept and the horizon is enlarged.

The trachelo-platysma is not found in any Mammal lower than a Primate (Ruge, *loc. cit.*) but in most Subprimates there exist in the neck two distinct superficial muscles: a deeper layer, the sphincter colli profundus, and a more superficial layer, the platysma, i.e. noto-platysma.

In Primates higher than the lemurs the sphincter colli profundus is absent or very rudimentary (Paugger(37)) and its place is taken by the trachelo-platysma which, according to Ruge (*loc. cit.*), is a fresh development in Primates, appearing phylogenetically for the first time. At the same time the noto-platysma begins to degenerate in two ways: (*a*) by losing its attachment to the lig. nuchae, (*b*) at a later period by losing its attachment to the face.

The lemurs occupy an intermediate position and often possess a sphincter colli profundus as well as a noto-platysma and trachelo-platysma. About the lemurs Ruge says (*Primaten*, p. 13):

> as the degenerate form of the noto-platysma and the small spreading out of the platysma (i.e. trachelo-platysma) over the neck and chest usually occur together, we feel we are right in assuming that a high degree of development of the muscle was a condition originally present in all prosimians... the spreading of the platysma over the chest and back of the neck is a standard condition for the primates.

But is this degeneration so certain? That the noto-platysma shows signs of degeneration may be true, and in keeping with the observed fact that this often coincides with the arrival of the trachelo-platysma. To what extent this is true of the trachelo-platysma is more uncertain; for if the fibres do not reach or approach the clavicle-shoulder region but end midway in the neck, it becomes very difficult to say whether the fibres are trachelo-platysma or merely abbreviated noto-platysma. But if the muscle be trachelo-platysma, is the muscle degenerate or immature? A good craniad but deficient caudad development would explain the condition found in some lemurs.

Again, though the arrival of the trachelo-platysma in Primates heralds the disappearance of the sphincter colli profundus, a subsequent degeneration of the trachelo-platysma does not induce a reappearance of the sphincter; e.g. in *Homo sapiens* it is not uncommon to find small or degenerate platysmae, but it is a rarity to find any trace of a sphincter colli profundus. So the possession of a sphincter colli profundus by all lemurs (except *Propithecus diadema*, which has neither trachelo-platysma nor sphincter colli profundus) would make it improbable that they had ever possessed well-developed trachelo-platysmae.

Noto-platysma

The origin of this muscle may be from the fascia of the neck, and reach neither to the shoulder nor to the lig. nuchae, e.g. some lemurs (Ruge, Halbaffen); or the origin may be from the posterior surface of the shoulder and the fascia of the neck for a variable distance between the lig. nuchae and the acromion-ear line, e.g. orangs, gorilla and chimpanzee; or a variable number of its fibres may reach and take origin from the lig. nuchae, e.g. Cercopithecidae. In this latter case those fibres attached to the lig. nuchae are divided into three distinct layers—a superficial, an intermediate and a deep—and each of these layers is continuous with a fibrous or fibro-muscular layer covering the occiput. The superficial layer of the noto-platysma is continuous with a very strong fibrous occipital layer; the intermediate layer represents the M. cervico-auriculo-occipitalis which postero-medially is continuous with a strong layer of occipital fascia; and the deep layer of the noto-platysma is directly continuous with the fascia covering the M. trapezius which, though attached to the nuchal line, appears to be on the same morphological plane as the M. occipitalis. The two superficial layers of the occipital fascia and the M. occipitalis terminate together in that layer of the galea to which the M. frontalis is attached. Ruge contended, and most writers have supported him, that the auricular and occipital muscles were off-shoots of the noto-platysma. Support is given to this by the condition found in the Cercopithecidae.

Trachelo-platysma

The origin of this muscle may be from the fascia of the neck cephalad to the clavicle, in which case it may be difficult or impossible to determine whether the fibres belong to the trachelo-platysma or are abbreviated noto-platysma fibres, e.g. some lemurs; or the origin may be from the anterior surface of the shoulder and from the thoracic wall at the level of the clavicle, e.g. *Homo*; or the origin may be from the anterior surface of the shoulder and from a large area of the thoracic wall extending even as far as the xiphisternum, e.g. orangs.

Bluntschli (1909) further subdivided the platysmal sheet into two portions, based upon the method of its insertion, viz. (1) the pars aberrans or that portion of the muscle which is inserted craniad to the angle of the mouth and may be called the pars supra-angularis, (2) the pars labialis which is inserted

lateral and caudad to the angle of the mouth. This term is misleading since not more than one-fourth to one-third of the fibres reach the lips. The term pars infra-angularis not only would be more accurate but would abolish the confusion between the terms pars labialis and portio labralis. More recently Paugger (37) has described in detail the platysma and, ignoring the phylogenetic and basic divisions of the older German school, takes with an altered nomenclature Bluntschli's subdivisions as his basis for a primary division of the muscle; regardless of the fact that the constituent fibres of the partes aberrans and labialis vary in the different species of Primates.

The pars supra-angularis needs no further subdivision, as it plays no complex part in determining the facial movements. But consideration of the pars infra-angularis shows that it is inserted in four different ways, each of which must have a different function. The four following subdivisions denote this and simplify description of the muscle:

(*a*) The *portio decussata*[1] comprises those fibres which decussate in the antero-medial plane caudad to the chin. It may be a very large sheet of muscle and be comprised of a portion of the noto-platysma and the whole of the trachelo-platysma, of the whole of the trachelo-platysma fibres (Z O 4), of a large portion of the trachelo-platysma fibres (Z O 3), or it may be absent as often in lemurs and man.

Ruge says (*Primaten*, p. 11):

> In Cynocephalidae, Cercopithecidae and the Stummelapes the crossing of the platysma is due to adaptation to the cheek pouches, and the amount of the crossing varies as the size of the pouches...the crossing of the platysma bundles merely indicates a more powerful development of the muscle and is not a fundamental arrangement. If we are right in conjecturing that in Platyrrhines the platysma crossing is closely bound up with the growth of the cheek pouches, and if the crossings in Catarrhines and man are derived from these, then these latter once must have possessed a cheek pouch. There is no evidence of this.

This author was very unwilling to allow that the Cercopithecidae belonged to the anthropoid stem, and hence regarded them as unsuitable for purposes of comparison. Paugger (*loc. cit.*) fully discusses the question of the crossing of platysmal fibres in the neck and pays special attention to those found in the Cerco- or Cyno-pithecidae. He does not agree with the attitude of Ruge towards these Primates. In the present dissection of two Cercopithecidae three facts emerged with great clearness. (1) The pouches did not appear to affect in any degree the facial musculature. They appeared rather as herniae of the buccal mucous membrane which, if not too large, remained more or less clothed by the M. buccinator; but, if large, the distal portion remained quite bare of any muscle tissue. This was especially noticeable in the large right pouch of Z O 5 (dioptogram E 3). It was to the neck only of the pouch that other muscles were found attached. (2) That few of the crossed platysmal fibres ended in or on the cheek pouches, which easily were lifted cranially without affecting the

[1] It must be noted that this term is applied to the insertion and not to the origin of the fibres of the platysma.

musculature (e.g. dioptogram E 3). In Paugger's (*loc. cit.*) careful drawings of his dissections some crossed platysmal fibres are seen to end upon the distal part of the cheek pouches, but the main body of fibres ends elsewhere. (3) That though Z O 5 had, relatively if not actually, the larger pouches it had relatively much smaller and less highly developed crossed platysmal fibres ending in the facial region. Therefore there seems no valid reason, why the appearance of buccal herniae should prevent the facial musculature of these Primates from being regarded as, more or less accurately, representing that possessed by the predecessors of the higher Primates.

Also the following observation would apparently suggest that the crossing of the trachelo-platysmal fibres is a fundamental one when it first appears. In the Subprimates are found, so far as can be gathered from the literature, only one portion of the platysmal sheet, viz. the noto-platysma, but its portiones modiolaris and labralis are always present and the latter meet, if they do not decussate, at the chin in the antero-median plane. If now, in Primates, a muscle arises anterior to but in the same plane as the noto-platysma, viz. the trachelo-platysma, its fibres must be forced medially and, if of any length, form a portio decussata.

(*b*) The *portio labralis* comprises those fibres which enter the lower lip and form labial tractors.

(*c*) The *portio modiolaris* comprises those fibres which end in the modiolar area. In the Primates other than man there is no true modiolus or agger musculosus, as the lips need not attain such precision of fine movements as is necessary for the production of speech. In these Primates the interlacing of the homologous muscles is much less intimate, and the insertions are distributed over a much wider area. This has been called the modiolar area as it still resembles the nave of a wheel, but a flatter and larger one than in *Homo*.

(*d*) The *portio mandibularis* consists of those deeper fibres which gain insertion into the mandible. Their presence or absence apparently depends upon the evolutionary position of the Primate, rather than upon the degree of development of the platysma of that Primate.

An attempt was made to construct a chart for comparing the platysmae of the Primates under dissection. The result was intriguing, so it was extended to embrace such other Primates as had been described with sufficient detail, e.g. chimpanzee, gorilla and lemur from Ruge, *Tarsius* from Wollard and Burmeister and the dog from Huber.

To the left of the schema[1] have been arranged outlines of the heads of four Primates with the various portions of the platysma indicated. The heads have been arranged in genealogical order and it will be seen that there is an homologous gradation in the platysma.

The lemur possesses a noto-platysma only, *Homo sapiens* a trachelo-platysma only, whilst the baboon and orang possess both types of platysmae. In the baboon the trachelo-platysma is confined to the portio decussata,

[1] Fig. 2. The outline of the lemur is after Ruge.

whereas in the orang the trachelo-platysma embraces the whole of the pars infra-angularis. The schema itself consists of two diagrams, the upper representing the origin, and the lower the insertion of the platysma together with its relationship to the lig. nuchae (fig. 2).

Upper diagram. X = xiphisternum. O = inion or occiput. (A) = tip of acromion.

The vertical and horizontal lines through these points represent similar lines on the cadaver. Thus the vertical line through (A) will closely correspond to the line joining the external auditory meatus to the tip of the acromion—a line frequently used by Ruge—whilst the horizontal line through (A) will correspond approximately to the line of the clavicle. All lines to the left of (A) will represent trachelo-platysma, and all lines to the right noto-platysma fibres. Ruge thought there was a definite relationship between the approximation of the platysma to the ligamentum nuchae and the evolutionary position of the Primate possessing such a platysma. This is clearly seen in the diagram.

Lower diagram. The vertical lines have the same significance as in the upper diagram, but the horizontal lines have no relationship to the cadaver; the horizontal interspaces represent the different portions into which the platysma has been subdivided. Different types of lines were selected for the different Primates, and the portio mandibularis platysmae was indicated by the ovoid thickening on the lines.

The key to the position to be occupied by the platysma of any particular Primate was obtained from the point of meeting in the face of the trachelo- and noto-platysmae, which was determined by following a muscle fasciculus from the acromion to the face. In Z O 1 and Z O 2 it was at the cranial margin of the portio modiolaris; in the gorilla, *Tarsius* and the orang described by Sullivan and Osgood it was in the middle of the portio modiolaris; in the chimpanzee and Z O 3 at the caudal margin of the portio modiolaris, etc. The more highly developed the Primate the smaller and less important becomes his noto-platysma, and the platysma seems to reflect faithfully its owner's position in the genealogical tree.

In the five Primates dissected there was a well-developed and extensive platysmal sheet consisting of both noto- and trachelo-platysma. No line of separation existed between these but the one gradually merged into the other. The direction of the most craniad fibres of the noto-platysma was almost horizontal, whilst that of the most median fibres of the trachelo-platysma was almost vertical, and there was a gradual transition from one direction to the other. The space in the antero-median plane between the platysmae was never very great, and there was a well-developed interweaving or intercrossing of the fibres from the opposite side, superficial and caudad to the simian shelf. The whole sheet thus formed an almost complete investment for the neck and side of the face.

Orang Z O 1. Noto-platysma

Origin. This was from the fascia at the back of the neck and shoulder. Distance from postero-median plane = 3·0 cm.; greatest thickness (inferiorly) = 0·10 cm.; width of muscle below ear = 3·0 cm.

Insertion. All the fibres enter the pars supra-angularis. The upper fibres run at first horizontally, but anterior to the ear they curl cranially and lie superficial to the Mm. orbito temporalis and malaris (A 2). The more caudal fibres end posterior to the M. malaris.

Aberrant fibres. In the region of the left shoulder there is a thin sheet of muscle, which lies superficial to the trachelo-platysma and crosses it at right angles (dioptograms A 1, A 2, A 3). This thin sheet arises from the region of the acromion process and the anterior surface of the shoulder joint, and runs caudally and medially towards the sternum but never reaches the middle line. On the right side there are no such aberrant fibres, but three well-marked muscle slips run, deep to the trachelo-platysma, transversely across the front of the neck from near the axilla to reach the middle line of the neck.

Trachelo-platysma

The right side is not as well developed as the left; it does not extend so far over the chest neither does it cover the air sac in the axillary region.

Origin (left side). From the chest wall as low as a point midway between the manubrium sterni and the xiphisternum, and thence to the acromion process. It almost completely covers the laryngeal pouch which in this specimen extends into the axilla.

Insertion. Comprises the whole of the pars infra-angularis, and it will be described under the various subdivisions of this.

(*a'*) *Portio decussata.* The majority of the superficial fibres of the trachelo-platysma medial to the shoulder region take part in this decussation, which is a very intimate and somewhat complex one. It was not possible to say that one set of fibres lay superficial to those of the opposite side. The decussation takes place in the region of the mental shelf, and after decussation each set of fibres reforms into two well-marked sheets of muscle, which cross the lower margin of the mandible and then diverge from each other. The more medial of these sheets spreads out fanwise and completely covers a large portion of the inferior labial tractors; cranially the lateral fibres of this sheet almost touch the M. triangularis. The more lateral sheet crosses the mandible lateral to the mentum, and turning craniad blends with the fibres of the Mm. caninus and orbicularis oris below or at the modiolar area. Here it is impossible to differentiate the fibres of the muscles concerned. The most lateral of these fibres have lost all connection with the portio decussata and apparently take origin from the fascia of the platysma. They end in two ways; the more medial by interlacing intimately with the M. caninus, and the more lateral by ending on the fascia of the platysma caudad to the M. malaris.

(*b'*) *Portio labralis.* This is formed by superficial fibres which cross the mandible; they cover the whole of the chin and most of the lower lip. The most medial fibres intermingle freely in the middle line with those of the opposite side, but the most lateral fibres do not extend as far as the angle of the mouth. Elsewhere they completely hide from view the M. orbicularis oris, and to gain the face pass deep to the M. triangularis. They are not to be separated from the underlying M. quadratus labii inferioris.

(*c'*) *Portio modiolaris.* These fibres end some distance lateral to the angle of the mouth in the modiolar area where they interlace with the Mm. buccinator, triangularis, orbicularis oris and caninus. They pass deep to the M. triangularis. The total width of this portion of the muscle at the modiolar area is only 1·35 cm.

(*d'*) *Portio mandibularis* is formed from the deeper fibres of the portiones decussata and labralis. Medially these fibres are inserted into the posterior margin and inferior surface of the mental shelf and the inferior margin of the mandible; laterally into the lateral surface of the mandible (dioptograms A 7, A 8). A few fibres only cross in the median plane. The insertion measures 3·75 cm. in length and 0·45–0·80 cm. in breadth.

Orang Z O 2

The trachelo-platysma fibres are longer, more powerful and more numerous than those of the noto-platysma.

Noto-platysma

Origin. From the fascia at back of the neck and shoulder; distance from postero-median plane = 4·36 cm. (sup.) = 3·0 cm. (inf.); width below ear = 4·3 cm.

Insertion. All the fibres enter the pars supra-angularis. Upper fibres are short, are horizontal in direction and have no craniad curl; they do not reach either the M. orbito temporalis or the M. malaris.

Trachelo-platysma

Origin. From the fascia of the chest wall midway between xiphisternum and manubrium sterni, and thence laterally to acromion process. It covers the major portion of the air sac, but in this subject the sac does not pass into the axilla. The gap in the fibres shown in the dioptogram is anterior to the shoulder, and is not the division between the noto- and trachelo-platysma. The three strips indicated in the diagram were tendinous, and extended very far caudally over the chest wall. Greatest distance in antero-median line separating the two muscles = 8·8 cm.

Insertion. This comprises the whole of the pars infra-angularis and is best described under its four subdivisions.

(*a'*) *Portio decussata.* The major portion of the fibres which take origin medial to the shoulder girdle take part in this decussation or crossing of fibres. Except for a small area at the symphysis menti there is little blending of the fibres of the two sides, though the crossing begins 2·6 cm. caudad to the posterior margin of the simian shelf. Moreover, a small percentage only of the crossed fibres from the right side remain superficial and end in the fascia of the chin; the majority of them become attached to bone, and will be described under the portio mandibularis. The superficial fibres of the left side cross the middle line superficial to the fibres from the right side, and end by intertwining with those fibres, or are inserted into the fascia of the right side of the face.

(*b'*) *Portio labralis.* These fibres cover the chin and lower lip. In the antero-median line they interlace freely with similar fibres from the opposite side, and extend laterally to within 0·75 cm. of the angle of the mouth. Lateral to this the M. orbicularis oris is visible over a small area. The fibres pass deep to the M. triangularis, which, in this subject, took its origin from the fascia of the platysma.

(*c'*) *Portio modiolaris.* These fibres pass deep to the M. triangularis and end in the modiolar area. The more superficial fibres end cranially by interlacing with the M. triangularis and M. malaris, and caudally with the M. orbicularis oris. The deeper fibres interlace with the M. buccinator slightly caudad and 2·45 cm. lateral to the angle of the mouth.

(*d*) *Portio mandibularis.* It is especially large in this subject, and the method of insertion is unusual and very different for the two sides.

Left side. This is comprised of the deeper fibres of the portiones decussata and labralis of the left side. They are inserted into the left antero-inferior margin of the mental shelf, for a distance of 2·0 cm. from the symphysis menti and immediately anterior to the fibres from the right side. Lateral to this the fibres are inserted obliquely into the lateral surface of the mandible, for a distance of 3·0 cm. from the symphysis menti.

The *right side* is comprised of the deeper fibres of the portio labralis, and the majority of the fibres which take origin from the right side of the chest. A few of these remain superficial to form to portio decussata, but for the most part they gain attachment to bone. Medially they gain attachment to the whole of the posterior edge of the mental shelf, and to five-sixths of the inferior surface of that shelf for a distance of 2·0 cm. on both sides of the middle line. Lateral to this they are inserted obliquely into the lateral border of the mandible, for a distance of 3·5 cm. lateral to the symphysis menti, i.e. to a point immediately beneath the space between the second premolar and the first molar tooth.

Orang Z O 3. Noto-platysma

This constitutes the pars supra-angularis and the portio modiolaris of the pars infra-angularis.

Origin. It arises by muscle slips from the deep fascia of the side and back of the neck, and, near the trachelo-platysma, by tendinous fibres from the spine

of the scapula. No fibres reach the lig. nuchae, and the most craniad are 6·0 cm. distant from the postero-median plane. The fascia, which is on the same plane as the muscle, is very thin and delicate.

Insertion. This will be described under its two heads.

The *pars supra-angularis* fibres end in the region of the cheek. The most craniad fibres at first run almost horizontally, but in front of the ear they curl cranially and partially cover the fibres of the M. orbito-temporalis.

The *portio modiolaris* is 2·90 cm. in width and 0·50 cm. in thickness. Its superficial fibres end in the modiolar area by interlacing with the superior labial tractors, M. orbicularis oris, M. incisivus superior and M. buccinator. Some fibres pass deeply between the bundles of the M. buccinator and are attached to the basis modioli (dioptograms C 1, C 3, C 9).

Trachelo-platysma

When the head was first freed from epidermis and the panniculus incarnosus, it appeared as if all the fibres of the lateral half of the platysma ended at the mandible (dioptograms C 2, C 3), and that the inferior labial tractors consisted of M. quadratus labii inferioris alone. This was not the case; the panniculus incarnosus here had a linear thickened band, with strips dipping deeply between the muscle fibres to become attached to the mandible. Thus a series of fibrous bridges or arches was formed, which constricted the muscle fibres and made them more tendinous in appearance. When these arches were cut through a thin sheet of platysma fibres was found to enter the lower lip.

Origin. From the xiphisternum medially, and obliquely across the chest as far as the tip of the acromion. The fibres of this sheet decussate with those of the opposite side, both in the region of the chin (portio decussata) and of the xiphisternum. Between these points of contact the muscle edges diverge, leaving an oval area filled with fibro-fatty tissue but devoid of superficial muscle. This gap measures 1·72 cm. at its widest point and is 6·50 cm. in length. The decussation at the xiphisternum consists of a few fibres only.

Insertion. This comprised only three portions of the pars infra-angularis as the portio modiolaris is composed of fibres from the noto-platysma. To take these seriatim:

(*a'*) *Portio decussata.* This large decussation begins 5·15 cm. caudad to the mental shelf and opposite the thyroid cartilage. The fibres run from the chest wall obliquely craniad, and, crossing the labial tractors at an acute angle, end in the mental region. They do not join or become part of the labial tractors; neither is there any tendency for the fibres to join up with the M. caninus or M. orbicularis oris fibres. The fibres of the right side lie superficial to the left. These decussating fibres end in two ways; the superficial seem just to fade away into the panniculus in the mental region, whereas the deeper are firmly attached to the posterior margin of the mental shelf. These latter will be more fully dealt with under the portio mandibularis.

(*b'*) *Portio labralis.* This is formed by the remainder of the superficial fibres of the trachelo-platysma, which passes over the mandible to be inserted into the chin and lips as in Z O 1 and Z O 2. It is unseparable from the underlying M. quadratus labii inferioris.

Portio mandibularis is comprised of the deeper fibres of the trachelo-platysma which gain insertion into the mandible. The fibres from the right side cross for a distance of 0·65 cm., whilst the left fibres cross for a distance of 0·70 cm. Thus the amount of crossing of fibres is very small. The more medial fibres are inserted into the posterior margin of the mental shelf, and there is a medial gap of 0·65 cm. quite devoid of muscle fibres. Laterally the fibres are inserted into the lateral surface of the mandible, to a point vertically beneath the posterior margin of the first molar tooth and 5·60 cm. from the symphysis menti.

Orang Z O 4

The platysma was phenomenally developed, was coarse fibred and its average thickness was 0·10 cm. The noto-platysma was equally powerful throughout its length, whereas the trachelo-platysma appears as a very thin sheet at its wide area of origin, and becomes thick and powerful as its fibres converge to the crossing in the middle line of the neck. The platysma covers the whole of the nape of the neck from the occiput to the upper dorsal region, the region of the shoulder and the sides and front of the neck, with the exception of a small triangular area whose base was 3·0 cm. at the supra-sternal notch and whose apex was 2·0 cm. cephalad to this notch. It thus formed an almost complete investment for the neck, and in addition it covered the whole of the chin and lower lip and much of the lateral surface of the face. Anteriorly the muscle split into several layers, due to a well-marked and singular crossing of the fibres in the middle line; posteriorly it split into three well-marked layers. The trachelo-platysma is exceptionally large; and yet the noto-platysma retains its origin from the whole length of the lig. nuchae, remains a more powerful muscle than the trachelo-platysma, and keeps possession of the major portion of the strategic pars infra-angularis. These attributes make this Primate an ideal basis or standard for the Primates for the study of the facial musculature, and any hesitation in so doing is due to Ruge's (*loc. cit.*) objections on the score of the cheek pouches. These objections already have been dealt with and more details will be supplied presently.

Noto-platysma

Origin. From the middle line of the back of the neck and upper dorsal regions; for the major portion it is from a median raphe, though near the occiput this expands into a short tendinous sheet. It may be said to take origin from the lig. nuchae.

In the region of the occiput three distinct layers are seen (dioptograms D 5 and D 6) a superficial, an intermediate and a deep, and each layer of muscle is continuous with a corresponding layer of epicranial fascia. These three fascial

layers unite to form the superficial layer of the galea, at the place where the M. occipitalis is inserted into this layer of the galea. The superficial and deep muscle layers of the platysma can easily be separated, over a comparatively small triangular area in which lies the intermediate or middle layer. This area is in shape almost an isosceles triangle, with the apex caudad and distant 4·7 cm. from the inion, whilst the base is slightly caudad to the nuchal line and 3·9 cm. in length. The deep layer does not reach as far as the nuchal line being 0·50 cm. caudad to it; in the space between the nuchal line and the craniad margin of the deep layer can be seen the fascia covering the oblique fibres of the M. trapezius, which extends as a muscular sheet right up to the nuchal line even in the middle line of the neck. The perimysium of this deep layer of the platysma is directly continuous with the layer of thick fascia which covers the upper portion of the M. trapezius, and this fascia is contiguous cranially with the fascia of the M. occipitalis. It appears that the M. occipitalis and the deep layer of the platysma are on the same morphological plane. These three layers of the platysma and their corresponding fasciae are well developed and distinct from each other.

Superficial layer. The fibres of this muscle sheet run forwards and slightly cranially, and are directly continuous in the region of the occiput with a stout layer of connective tissue that is on the same morphological plane as the M. frontalis. The most craniad fibres of this muscle sheet form a bundle distinct from the remainder; it runs auralwards, and, crossing the M. auricularis posterior, is inserted into the eminentia conchae in common with the most lateral fibres of the middle layer of the noto-platysma, to which it runs parallel and is closely applied.

Middle (intermediate) layer represents the M. cervico-auriculo-occipitalis. It is figured by Ruge for a baboon (*Primaten*, Tafel ii, fig. 17) and is called by him the nuchal portion of the M. auriculo-occipitalis. It apparently corresponds with the cervico-auriculo-occipitalis of Huber (*Morph. Jahrb.* Bd. LII, Heft i, pp. 16–18). It is a broad and powerful band of muscle 0·10 cm. thick, 2·9 cm. wide and 6·4 cm. in length. It takes origin like the previous layer from the lig. nuchae, and has therefore no real attachment to the occipital bone. At their origin the most caudal fibres of this layer are closely interwoven with those of the deep layer of the platysma, though for the major part of their origin these layers are quite separate. Likewise it is quite distinct from the superficial layer already described. The fibres run obliquely craniad and laterally, and their insertion embraces the posterior edge of the M. auricularis superior. The majority of the fibres seem to lie deep to this muscle; of the remainder only the lateral ones proceed for any distance across the surface of the M. auricularis superior; they cross the root of the ear to end in the fascia of the M. orbito-temporalis. A very few of the most lateral fibres seem to gain an insertion into the eminentia conchae, in conjunction with the band of the superficial layer of the platysma.

Deep layer. These fibres form a powerful sheet which takes origin from the

lig. nuchae. Running at first transversely, they soon become oblique and lie parallel to the superficial layer; this they eventually join to form a common sheet which ends in the upper cheek region.

Insertion. This comprises the whole of the pars supra-angularis and the portiones labralis, modiolaris and mandibularis of the pars infra-angularis.

Pars supra-angularis. These fibres run at first horizontally, but anterior to the ear they curl cranially, to cover a large portion of the lateral region of the face and few fibres of the M. orbito-temporalis.

Portio labralis platysmae. These fibres are powerful throughout their course, and the thickness of the sheet is increased by the converging of the fibres towards their area of insertion. Towards their insertion the sheet splits into two layers, the one superficial and the other deep, with a very definite line of cleavage between them. This line of cleavage is broken by several successive bundles of muscle fibres passing from the more superficial to the deeper layer; whilst between these two layers will be seen the deep decussation fibres of the trachelo-platysma. Most though not all the fibres of the deeper layer are attached to the mandible, and will be described under the portio mandibularis platysmae; the remaining fibres pass freely over the margin of the mandible to become labial tractors, or else to decussate and end in the panniculus incarnosus in the region of the tuberculum menti. The fibres of the portio labralis platysmae as they approach their insertion become pale and more tendinous in character. Laterally they extend as far as the angle of the mouth and reach the lip margin, whilst medially they completely cover the chin and decussate with the fibres of the opposite side.

The inferior labial tractors are formed wholly by the portio labralis platysmae as there is no M. quadratus labii inferioris.

Portio modiolaris. These fibres pass on either side of the cheek pouches. Craniad to the cheek pouch is a large band 1·4 cm. in width. A few fibres end superficially by intertwining with fibres of the M. buccinator, M. incisivus inferior and M. caninus; the majority of the fibres pass between the fibres of the M. buccinator, to gain attachment to the mucous membrane of the neck of the pouch. Caudad to the cheek pouch the platysma fibres decussate with fibres of the M. buccinator, and gain attachment to the mucous membrane of the modiolar area deep to the neck of the pouch.

Portio mandibularis. The deeper fibres of the portio labralis platysmae alone find an insertion into bone; the area of attachment is very small due to the fibres running in a direction more or less parallel to the corpus mandibulae. The attachments are of two kinds: (1) a true attachment to bone of a few fibres, chiefly from the right side of the neck as these are more deeply situated. In this Primate the attachment is limited to the posterior free edge of the mental shelf. Most of the corresponding fibres of the left side end in the region of the right mental tubercle; (2) a false attachment to bone, where the fibres are not interrupted or broken but anchored in the region of the mental tubercles by strong fibrous tissue. Between the mental tubercles is a triangular bare area.

TRACHELO-PLATYSMA

This comprises the fibres of the portio decussata only.

Origin. From the front of the chest wall below the clavicle, and the front of the shoulder.

Insertion. This is very complex, and the left side lay superficial to the right at each crossing of fibres. Unlike the usual decussation seen in this region, the fibres after decussation curl laterally around the lower edge of the mandible, and then run cephalad to spread themselves fanwise over the sides of both cheeks, anterior and deep to the cheek pouches. These fibres are *not* attached to the cheek pouches; those passing anterior to the pouch interlace with the fibres of the M. caninus; those passing deep to the pouch seem to fade away on the fascia of the platysma. Deep to these fibres can be seen the fibres of the portio labralis proceeding towards the lip, and these two sets of fibres are now at right angles to one another. (Dioptograms D 2 and D 3 illustrate these points. In D 3 the finer fibres have been omitted and only the coarser fibres shown, so as to illustrate the relationship to the underlying labial tractors.) When the superficial decussation layer is dissected away, there is seen lying beneath it a similar but much more powerful sheet of fibres, which decussates freely between the fibres of the portio labralis platysmae. These fibres can be traced to a deep crossing of the fibres of the trachelo-platysma from the opposite side of the neck (see dioptogram D 4). For convenience these will be alluded to as the deep decussation fibres. These deeper fibres, like the portio labralis platysmae, differ from the other facial muscles and the remainder of the platysma, in that they are much paler in colour, and were shiny and semi-tendinous in character. The decussation fibres, especially the deeper layer, end by intermingling freely with the fibres of the M. caninus in the modiolar area. This condition probably represents the first stage in the formation of the M. triangularis.

Macaque Z O 5

The platysma was a miniature representation of that found in the baboon Z O 4 but not quite so well developed. The similarity in the occipital region was so marked that no extra dioptograms were necessary. The fascia in this region was much finer, its different layers more difficult to define, and cranially they were involved in the operation area.

NOTO-PLATYSMA

Origin. The cranial three-fifths take origin from the nape of the neck, but the lower portion of these fibres were destroyed in the removal of the spinal cord. The caudal two-fifths takes origin from the supra-spinatus region. In the nape region the upper portion of the noto-platysma consists of three layers, a superficial, a medial and a deep. The superficial layer reaches to within 1·0 cm. of the postero-median plane, and is directly continuous with a very strong facial or tendinous sheet which takes origin from the ligamentum nuchae. This fascia is continued over the occiput and reaches the operation area on

the scalp. It covers all the muscles of the posterior portion of the cranial dome. The deep layer takes origin from the ligamentum nuchae, but not as high as the inion from which it lies 1·10 cm. distant. Its upper edge lies parallel to the nuchal line and is united to it by a fine sheet of fascia. Through this can be seen shining the fibres of the M. trapezius similarly to that of the baboon Z O 4. The width of this deep layer is 1·0 cm., and it joins the superficial layer 3·65 cm. lateral to the postero-median line. Between these two layers is a small triangular gap, and in this the middle layer or M. cervico-auriculo-occipitalis takes origin from the ligamentum nuchae. This latter muscle pursues a course very similar to that found in the baboon Z O 4.

Insertion. This comprises the portiones modiolaris and labralis of the pars infra-angularis, and the pars supra-angularis.

Pars supra-angularis. This is supplied from the cranial three-fifths of the muscle fibres. These fibres barely cross the ear-mouth line and just reach the origin of the M. zygomaticus.

Portio modiolaris. This ends both craniad and caudad to the cheek pouch. Those fibres ending craniad to the pouch are derived both from the craniad three-fifths and the caudad two-fifths of the noto-platysma. They end in one of two ways; some end superficially in the modiolar area and decussate with the M. caninus and M. incisivus inferior, and others pass between the fibres of the M. buccinator which cover the pouch, and reach the mucous membrane on the dorsal or craniad aspect of the pouch. Those fibres which end caudad to the pouch and lie deep to it also end in two ways. Some pass between the fibres of the M. buccinator covering the pouch to end in the mucous membrane of the pouch, and the remainder enter the modiolar area caudad to the neck of the pouch (see dioptograms E 3 and E 9). All fibres which gain insertion into the pouch do so close to its neck, i.e. its emergence from the buccal mucous membrane, and no platysmal fibres are inserted into the belly of the pouch.

Portio labralis. This showed no peculiarities worthy of comment.

Trachelo-platysma

Origin. This is from the chest wall well below the clavicle, and the anterior surface of the shoulder. At its origin the sheet is not a continuous one but consists of several separate bands of muscle.

Insertion. These fibres form the portio decussata. There is a complete decussation of all the trachelo-platysma fibres in the middle line of the neck, the fibres of the left side being superficial to the right. The decussation fibres are all superficial and there is no deeper set as in the case of the baboon Z O 4. After decussation the majority of the fibres pass anterior to the cheek pouches to end in the modiolar area, where they interweave chiefly with the fibres of the M. caninus but also to a small extent with the portiones labralis and modiolaris. A few of the most anterior fibres pass deep to the portio labralis in the region of the chin and here they gradually disappear. Also a few of the most posterior fibres end at the neck of the cheek pouch.

MM. LABIORUM SUPERFICIALES

For the sake of convenience the portio labralis platysmae will be included with the inferior quadrate muscles when discussing their distribution in the lips. These three muscles, in the Primates dissected for this article, have insertions into the lips exactly homologous to that found in man. In these primates it has been a simple matter to demonstrate the sheet of muscle fibres which cover the M. orbicularis oris. In a section under the microscope the individual fibres are seen passing between the bundles of the M. orbicularis oris in a manner analogous to that seen in man. The muscles therefore must act as powerful labial tractors as has been shown to be the case in *Homo sapiens.*

M. QUADRATUS LABII INFERIORIS (2)

There is little to be noted about this muscle. Its presence or absence depended not only upon there being a portio mandibularis, but that this should be attached to the corpus mandibulae and not to the mental shelf alone. It was present in the orangs but not in the two lower Primates. But even in the orangs there was no line of cleavage between it and the overlying portio labralis platysmae, and the fibres of the two muscles could not be separated. Its presence was detected by the origin from the corpus mandibulae of certain fibres which had appeared to be deeper fibres of the portio labralis. Their distribution over the chin and lips is similar to the portio labralis platysmae.

Z O 1. Origin extends from 0·4 to 3·35 cm. from the median plane.

Z O 2. Origin is from the inferior surface of the mental shelf from the middle line lateralwards for a distance of 2·0 cm., and from the lateral surface of the corpus mandibulae for a further 1·0 cm. The distance separating the origin of this muscle from the insertion of the portio mandibularis platysmae is never greater than 0·30 cm.

Z O 3. Origin does not quite reach the middle line, and the gap between the origins of the two M. quadratus labii inferiores is 0·65 cm. The mode of origin was very similar to Z O 2, and the most lateral point of attachment to the mandible was 5·60 cm. from the middle line.

M. QUADRATUS LABII SUPERIORIS (3)

This series of dissections shows: (1) That in this macaque the caput infra-orbitale was so very insignificant that it might be called a "Rest." This primate, therefore, might be said to possess only the caput angulare, i.e. M. levator labii et nasi. (2) That in the baboon Z O 4 no trace could be found of the caput angulare and the only muscle present was a very large caput infra-orbitale (M. maxillo-naso-labialis). (3) That all the orangs possessed capita angulare et infra-orbitale; both capita were large and overlapped each other. However, the fibres of each ran in different directions and a definite line of cleavage lay between the muscle sheets. In Z O 1 and Z O 2 the conditions found resembled the baboon, in that the caput infra-orbitale formed the

major portion, if not the whole, of the fibres entering the upper lip; in Z O 3 both heads seemed equally represented in the upper lip. (4) That no caput zygomaticum was present. The caput zygomaticum and the M. zygomaticus arise from the large muscle sheet that extends from the auriculo-temporo-orbital region to the oro-labial region. In the orangs no fibres of this sheet gain any attachment to bone, so they possess neither a M. zygomaticus nor a caput zygomaticum. In the baboon this sheet attains two areas of attachment to bone; the auriculo-labial fibres have a true bony attachment and form the M. zygomaticus, and the temporo-labial fibres are attached to bone by dense fibrous tissue similarly to the platysma fibres. Probably it is an indication of a future true attachment to bone, but at present the muscle fibres are not interrupted and there cannot be said to be any caput zygomaticum. In the macaque there is no sign of attachment to bone of the temporo-labial fibres, but the auriculo-labial fibres have a true bony attachment, and we get a type of M. zygomaticus similar to that of the baboon.

Orang Z O 1

The capita angulare et infra-orbitale are well developed. At their origins from the orbital margin these two heads seemed to fuse, but more caudally (orally) there was a well-marked line of cleavage, containing areolar tissue, between them. This enabled the origins of the two muscles to be separated, though there was intertwining of muscle fibres.

Caput Angulare

This is a large, dark-coloured, fan-shaped muscle sheet lying in the same plane as the caput mediale M. malaris and the M. orbicularis oculi, from which it is separated by the angular vein. The muscle is 0·10 cm. thick at a point midway between the origin from the lig. palpebrae mediale and the insertion into the nose. Its fibres never could be confused with those of the caput infra-orbitale as they run in a different direction, lie superficial to and are slightly separated from the latter.

Origin. This is from the nasal process of the maxilla—medially as far as the naso-maxillary suture and laterally as far as the origin of the M. orbicularis oculi—, from the lig. palpebrae mediale, and from the infra-orbital margin for a distance of 1·30 cm. from the middle line (A 1). Two small slips from the M. frontalis and M. depressor capitis join the craniad portion of the caput angulare (see inset in dioptogram A 1).

Insertion. This is fan-shaped. The most medial fibres pass deep to the M. procerus and are attached to the bulb of the nose in the median plane. The intermediate fibres are attached to the whole of the ala nasi and form a levator alae nasi or dilator narium. The most lateral fibres are the most oblique and are inserted, for the most part, into the bucco-labial furrow. Some of the deeper fibres appear to interlace with the most medial fibres of the caput infra-orbitale, and thus may gain insertion into the upper lip.

Caput Infra-orbitale

Is a powerful dark-fibred muscle roughly quadrilateral in shape and 1·20 cm. thick.

Origin. From the infra-orbital margin from 1·30 to 3·1 cm. from the middle line. Medially it interlaces with fibres of the caput angulare, and laterally it is in contact with the cranio-lateral fibres of the M. orbicularis oculi which originate from bone.

Insertion. The muscle passes deep to the caput angulare and then spreads out fanwise to cover the upper lip, concealing the M. orbicularis oris and M. incisivus superior. Medially the terminal fibres curl around the nostril to reach the median plane; laterally they come in contact with and receive a small accession of fibres from the M. malaris.

Orang Z O 2

The caput angulare and caput infra-orbitale were both present.

Caput Angulare

This is a large coarse-fibred, red coloured muscle, easily distinguished from the M. procerus and M. orbicularis oculi, which were paler in colour. It was 0·15 cm. in thickness.

Origin. From the nasal bone and nasal process of the maxilla immediately craniad to the fossa pyriformis, and for a distance of 0·90 cm. above this. These fibres reach the middle line, and interlace with fibres from the opposite side and also with the M. procerus. Craniad to this the origin becomes more lateral, until it reaches the orbital margin caudad to the fronto-maxillary suture. The remainder of the fibres take origin from the orbital margin, the most lateral of which are 1·65 cm. from the middle line.

Insertion. The medial fibres enter the region of the ala nasi, and the remainder enter the panniculus incarnosus lateral to this at the bucco-labial furrow. No fibres were traced into the lip area.

Caput Infra-orbitale

This resembles the caput angulare in colour, strength, and the coarseness of its fibres. Its thickness near its origin is 0·16 cm. It passes deep to the caput angulare; its median fibres curl around the nostril to reach the middle line 1·30 cm. caudal to the nostrils; its lateral fibres adjoin those of the M. malaris and run obliquely to reach the lip margin 0·50 cm. medial to the angle of the mouth. The muscle sheet thins out towards its insertion where it covers almost the whole of the upper lip.

Origin. From the infra-orbital margin 1·60 to 3·52 cm. from the middle line. Thus the overlapping of the two heads is to a small extent only. Its origin was completely concealed by the M. orbicularis oculi.

Orang Z O 3

Capita angulare et infra-orbitale are well developed and dark-coloured; some fibres overlap and intertwine at their area of origin.

Caput Angulare

The muscle is 2·0 cm. thick, dark in colour, and its surface displays shiny silver-like bands of fibrous tissue. The muscle lay in the same plane as the M. orbicularis oculi.

Origin. Its most lateral fibres overlap and interlace with the most median fibres of the caput infra-orbitale. It takes origin from the edge of the nasal bone, from the nasal process of the maxilla, from the nasal process of the frontal bone and from the orbital margin for a distance of 2·0 cm. lateral to the middle line. On the right side some medial fibres of the M. frontalis join and form part of the medial edge of the caput angulare, on the left side similar fibres of the M. frontalis join the M. depressor capitis.

Insertion. From its area of origin the muscle spreads into a large fan-shaped sheet. The most medial fibres spread across the medial plane to interlace with their fellows of the opposite side, the right fibres being superficial to the left; no trace of a true M. procerus was found. The intermediate fibres spread out upon the ala nasi, and the lateral fibres curl around the nose some to end in the bucco-labial furrow, but the majority to reach the upper lip as labial tractors. The lateral half of the fibres, a little craniad to their insertion into the ali nasi and their appearance in the upper lip, are closely interwoven with and inseparable from the underlying fibres of the caput infra-orbitale.

Caput Infra-orbitale

A broad sheet of muscle 0·20 cm. in thickness, of a darker colour than the caput angulare and lacking its fibro-tendinous strands.

Origin. This is from the inferior orbital margin 1·58 to 3·75 cm. from the middle line.

Insertion. It is inserted into the ala nasi and the upper lip. Laterally the fibres of the M. malaris join themselves to the superficial surface of the muscle. As has been already noted there is a strong interlacement in the bucco-labial furrow with the fibres of the overlying caput angulare.

Baboon Z O 4

The muscle will be described as possessing only one head, viz. the caput infra-orbitale, though some doubt exists as to the presence in a primitive form of the caput zygomaticum. The caput infra-orbitale and the M. malaris lay in the closest contact and apparently formed a continuous sheet of muscle. One interfascicular space, deeper and more marked than the rest, was regarded as the probable line of their meeting. Between the two eyes and caudad to the lig. palpebrale mediale is a pentagonal area devoid of muscle, but filled with

fascia and small blood vessels. This was caused by the complete absence of a caput angulare, which, in its turn, may have been due to the large maxillary osseous ridges on the dog-like snout.

Caput Infra-orbitale

This is a powerful dark and coarse-fibred muscle whose thickness was 0·08 cm.

Origin. From the infra-orbital margin 1·0 to 3·0 cm. from the middle line. This was not only concealed by the overlying M. orbicularis oculi but the two sets of fibres were inseparably interlaced, and it was only by examining the deep surface of the caput infra-orbitale that its origin was manifested. Then it was seen that laterally there was a definite gap in the line of origin devoid of muscle tissue, and that a small band (0·45 cm.) of muscle lay lateral to this; these lateral fibres were intimately interlaced with those of the overlying M. malaris. It is possible that this may represent a primitive caput zygomaticum, but for the present it will be regarded as a portion of the caput infra-orbitale.

Insertion. The most medial fibres pass obliquely towards the mid-nasal region, where they interlace with fibres from the opposite side and with the M. procerus. These fibres are less powerfully developed and contain more veins in their midst than the remainder of the muscle. The intermediate fibres form a powerful band which is inserted into the ala nasi. The remainder of the fibres enter the upper lip and become labial tractors. The most medial of these curl around the nostril, and proceed towards the middle line a short distance below the nares.

Macaque Z O 5

The muscle in this Primate is represented by the caput angulare, as the caput infra-orbitale is so insignificant as to be easily overlooked and can possess no functional value. It is represented by a few weak fibres which took origin deep to the caput angulare from the infra-orbital margin 1·3 from the middle line. These fibres ran medially and orally and interlaced freely with the fibres of the more superficial muscle.

Caput Angulare

This is a very powerful muscle which appears to usurp the function of the M. procerus as well as that of the caput infra-orbitale.

Origin. From the nasal process of the maxilla, the medial palpebral ligament, and the infra-orbital margin for a distance of 1·40 cm. from the middle. Mediad and craniad to the lig. palpebrale mediale there is a strong fibrous arch protecting the angular vessels; the muscle takes origin from this also.

Insertion. Near their origin the most craniad fibres decussate freely with the M. depressor capitis. When they emerge from beneath the inferior margin of the M. depressor capitis they run almost vertically downwards in the median plane, and represent the M. procerus both in appearance and attachment (q. v.). No line of cleavage or demarcation could be found to separate these from the

remainder of the muscle fibres. The intermediate fibres gained the ala nasi, and the most lateral gained the labium superior to become the medial portion of the labial tractors. Laterally these fibres are in close contact with the M. malaris.

M. ZYGOMATICUS (4)

In the orang, as has been noted, there is no attachment to bone of those labial fibres which take origin in the region between the orbit and the ear; consequently there can be no M. zygomaticus. It is difficult to know whether this is a sufficient definition, or whether some regard should not be paid to the mode of the insertion as well as of the origin of the muscle. A true M. zygomaticus in that case would not only take origin from bone, but also would have some portion of its fibres inserted into the mucous membrane of the buccal or modiolar region. That the question is not merely an academic one is evidenced by the orang Z O 1, in whom some of the fibres of the M. orbito-labialis (M. malaris) have a definite insertion into the basis modioli though they have no bony origin; the difficulty would have been greater had they been attached to bone by strong fibrous tissue as in the baboon Z O 4.

Baboon Z O 4

The muscle is powerful, coarse fibred, and derived from the auriculo-labial rather than the temporo-labial fibres. It has a tendinous origin from the zygomatic arch, and its fibres run almost horizontally towards the angle of the mouth; as they approach the mouth they form a flat sheet, the craniad margin of which is in contact with the M. malaris and the caudad margin with the platysma. The sheet passes deep to the M. caninus and, for the most part, ends in the mucous membrane of the modiolar area, where it interlaces with fibres from the M. buccinator, portio modiolaris platysmae and M. orbicularis oris; a few of the most craniad fibres turn medially beneath the M. malaris, and end by joining the peripheral margin of the M. orbicularis oris. Further details of the insertion will be found in the description of the modiolar area.

Macaque Z O 5

This muscle is a powerful and well-developed though thin sheet (0·05 cm.), whose origin from the zygomatic arch is musculo-tendinous. Soon after its origin the muscle splits into two layers, a craniad and superficial which passes superficial to the M. caninus and becomes the labial tractor of the lateral portion of the upper lip, and a caudad and deep layer which passes deep to the M. caninus and ends in the submucosa of the modiolar area.

M. CANINUS (5)

Orang Z O 1

The muscle was well developed and dark fibred.

Origin. From the canine fossa caudad to the infra-orbital foramen, an area measuring 0·72 cm. sagittally and 0·41 cm. coronally. This ovoid

muscle mass, as it travels caudally, spreads out fanwise and becomes more superficial. Its superficial fibres intermingle freely and intimately with the caput laterale M. malaris; the majority of its fibres pass caudad to this muscle to lie superficial to the platysma, and form a striking superficial muscle in the modiolar area. These fibres mingle so freely and intimately with the portio decussata fibres of the platysma that it is impossible to distinguish the endings of either muscle. One muscle bundle passes deep to the platysma, and ends by intertwining with the fibres of the M. buccinator.

Orang Z O 2

A well-developed almost cylindrical muscle.

Origin. From the canine fossa caudad and lateral to the infra-orbital foramen, an area measuring 1·25 cm. sagittally and 1·75 cm. coronally.

Insertion. From this origin the muscle spreads out fanwise towards its insertion and becomes more superficial, but it does not break from under cover of the M. malaris. The cranio-lateral fibres proceed laterally to be inserted into the fatty tissue of the cheek anterior to the M. masseter. The medial fibres proceed caudally and laterally, and end in the modiolar area by interlacing with the M. buccinator, M. malaris and M. triangularis. A few of the most medial fibres turned oralwards to interlace with the fibres of the M. orbicularis oris lateral to the angle of the mouth. A few "anchor" fibres may have reached the lower lip.

Orang Z O 3 (dioptogram C 4)

This dark-fibred muscle was poorly developed in comparison with the other facial muscles.

Origin. From the canine fossa caudad to the infra-orbital foramen, an area measuring 0·50 sagittally and 0·65 coronally.

Insertion. Just inferior to the origin the muscle is only 0·25 cm. thick, and spreading out fanwise it runs caudally and medially. It ends in the modiolar area in three distinct layers: (*a*) a superficial very thin sheet crossing superficial and at right angles to the Mm. incisivus superior and orbicularis oris, (*b*) a still smaller thin fan passes laterally between the M. buccinator and M. orbicularis oris, to end by interlacing with the fibres of the M. buccinator at the same level as a few fibres of the platysma, (*c*) is deeply situated and more powerful than the other portions of the muscle. The fibres run medially and orally, and are inserted into the modiolar area medial and craniad to the M. buccinator (dioptogram C 9).

Baboon Z O 4

It is a powerful coarse-fibred muscle.

Origin. Is a linear or crescentic one from the canine ridge caudad and medial to the infra-orbital foramen, and measures 1·75 cm. The origin is musculo-tendinous.

Insertion. From its origin the muscle runs in a direction approximately parallel to the margin of the upper lip (dioptogram D 4), and lies along the craniad margin of the M. orbicularis oris and close to the bone. In this part of its course the muscle is covered by the caput infra-orbitale M. quadratus labii superior and the M. malaris, and measures 0·85 cm. in width and 0·10 cm. in thickness and 3·30 cm. in length. At the lateral margin of the M. malaris the muscle becomes superficial, and spreads out fanwise superficial to the M. zygomaticus. It forms one of the muscles of the modiolar area, and chiefly interlaces with the deep and superficial sheets of the portio decussata platysmae. The interlacing is not too intimate and allows the fibres of the two muscles to be distinguished from one another.

Macaque Z O 5

It is a powerful thick band of muscle resembling in many respects that seen in the baboon.

Origin. From the canine jugum caudad to the infra-orbital foramen.

Insertion. From its origin the muscle proceeds laterally in a direction almost parallel to the margin of the upper lip, lying close to the bone and deep to the labial tractors. It passes between the two portions of the M. zygomaticus, and immediately spreads out fanwise over the superficies of the modiolar area. Its chief interlacement is with the fibres of the portio decussata platysmae but it is not a very intimate one.

M. TRIANGULARIS (6)

The great variability of the M. triangularis in *Homo sapiens* had been recognised, but it was not anticipated that in the lower primates the difficulty would be to determine what fibres constituted a M. triangularis. It has been maintained that the M. triangularis is a new muscle appearing for the first time in and peculiar to man; but Ruge (41) has described Mm. triangulares in other Primates. Ruge (*loc. cit.*) maintained that the M. triangularis was a caudad extension of the fibres of the M. caninus or canino-orbicularis, which reached or became attached to the mandible. Huber supports this conception (*Morph. Jahrb.* Bd. LII, Heft i, S. 10). The objection to this is best stated by asking a physiological question, viz. Is it possible for a muscle fibril to be quiescent in one-half of its length and active in the other half? This never has been shown to take place and probably is impossible; and what is impossible for a single fibril is equally impossible for a sheet of muscle fibrils. The sheet may act in sections, but each section must act throughout its whole length. Such being the case, how can Ruge's theory of the genesis of the M. triangularis explain the muscle activities found in laughter? Here the M. zygomaticus and M. triangularis are powerfully contracted and scar the face as with a wheal, yet there is no sign of the M. caninus being active to even a small extent. On these grounds alone it seems advisable to abandon for the present Ruge's theory. Froriep (1877) (18), from a dissection of the human subject with very

abnormal facial musculature, first suggested that the M. triangularis was derived from platysmal fibres which crossed beneath the chin. Ruge (1887) (41) scathingly criticised this. W. Schmidt (1894) (43) collected a remarkable series of observations—again in the human subject—in support of Froriep's theory, and sought to show that not only the M. triangularis but also the M. transversus menti (caput transversum) were derived from those fibres of the platysma which crossed beneath the chin. Consideration of the conditions found in the five primates here described seems to strengthen materially this view.

In the orang Z O 3 none of the portio decussata platysmae fibres appear upon the face, and this Primate has been regarded as not possessing a M. triangularis. The absence of these crossed platysmal fibres has left exposed, better than any dissection could do, the fibres of the Mm. incisivus superior and orbicularis oris as they terminate normally upon the platysmal fascia (dioptogram C 2); it has a superficial resemblance to a M. triangularis, but the distal fibres cannot function separately from the M. orbicularis oris.

In the macaque Z O 5 the crossed platysmal fibres end in the modiolar region (dioptograms E 2, E 3, E 4), but they remain distinct from, though interlacing with the fibres of the M. caninus. These fibres have no attachment to the mandible. In the baboon Z O 4 is seen a further step towards the formation of a M. triangularis. Here the crossed platysmal fibres are in two layers, a superficial and a deep (dioptograms D 2, D 3, D 4), and each interlaces in the modiolar area with the fibres of the M. caninus. The interlacement here is more intimate and larger than that seen in the macaque, but again there is no attachment of the platysmal fibres to the mandible.

In the orang Z O 1 is seen a further stage, in as much as the crossed platysmal fibres are so intimately blended in the modiolar area with those of the M. caninus that it is impossible to separate the one from the other. Though the main body of the crossed platysmal fibres still retain their connection with the platysma of the opposite side, one small sheet of fibres situated more laterally upon the cheek has lost inferiorly all connection with the platysma, whilst superiorly it ends in two ways; the more medial fibres interlace with the M. caninus, and the more lateral end blindly upon the fascia of the platysma. Again, in this orang may be seen those crossed fibres of the platysma which pass medial to the M. triangularis and end in the region of the lower lip, apparently corresponding to the M. triangulaire interne (Cruveilhier). None of the platysmal fibres appearing upon the face are attached to the mandible.

Finally in Z O 2 there is a thin sheet of superficial fibres which neither freely interlaces nor is directly continuous with any other muscle. It arises from the fascia of the platysma near the lower border of the mandible, and ends in the modiolar area lateral to the angle of the mouth. Apparently these are crossed platysmal fibres that have lost all connection with the parent body, similar to the lateral sheet of fibres in the orang Z O 1, and would therefore represent a true caput latum M. triangularis (*Journ. Anat.* vol. LX, part 1, pp. 17–18). When the weight of this series of observations in Primates other

than man is added to those observed in man by Froriep and Schmidt, the balance seems to incline to the theory that the M. triangularis, with its caput transversum, is an offshoot of the new muscle found in Primates, viz. the trachelo-platysma.

Closely bound up with this question is that of the genesis of the M. risorius. The understanding of this muscle is aggravated by the great variety of musculi risorii described in the literature, and it might be well to divide them according to the direction of their fibres into three main groups, viz. cranio-labial, transverse and caudo-labial. Even then the position is an unsatisfactory one, for not only is the name risorius a misnomer, but at times it is difficult to know what fibres should be called a M. risorius, and to distinguish between the so-called platysma-risorius and triangularis-risorius. This distinction is supposed to depend upon the relationship of the risorius fibres to the M. triangularis, i.e. whether they lie deep or superficial to this muscle (Ruge (41)). But in some cases the M. risorius seems to join the lateral edge of the M. triangularis. Again, if there is uncertainty as to the composition and genesis of the M. triangularis, is it possible or permissible to derive from it another equally elusive muscle? The variability of the M. risorius is much greater than its utility, and may not this variability be the clue to its genesis, for what so variable as a "Rest"? but a "Rest" of what? (*a*) The portio decussata of the trachelo-platysma at once suggests itself, in as much as the M. risorius of Santorini is said to be a derivative of the M. triangularis. The only types of M. risorius accounted for by this theory are those mentioned by Bluntschli (*Morph. Jahrb.* Bd. XL), where the fibres of the M. risorius lie superficial to or run parallel with the fibres of the M. triangularis, i.e. the caudo-labial group of risorii. It is difficult to regard these fibres as Mm. risorii; they appear more akin to the capita latum et transversum M. triangularis and the M. triangulaire interne (Cruveilhier), which lie on either side or superficial to the M. triangularis. In this connection it must be remembered that in the orang Z O 1 the M. triangulaire interne is derived from the crossed platysmal fibres, and that in the baboon Z O 4 there were superficial as well as deep crossed platysmal fibres forming the primitive M. triangularis. (*b*) Another muscle in this region which might form "Reste" is the noto-platysma. In Primates the portio modiolaris of the noto-platysma may lie either superficial to, deep to, or on the same plane as the M. caninus or the trachelo-platysma (cf. Ruge, Paugger, etc. *loc. cit.*), so the vexed question about the relative level of the M. risorius does not obtrude itself. The idea of the existence of such "Reste" is encouraged by the relations to each other of the noto- and trachelo-platysma, and by their phylogenetic histories. The noto-platysma is driven back by the invading trachelo-platysma, and evacuates one after another the strongholds of the pars infra-angularis; the last to be surrendered is the portio modiolaris. If a "Rest" remain it is here or in the pars supra-angularis that such would be found. "Reste" of the pars supra-angularis are well recognised, so why not of the portio modiolaris? The transverse group of risorii, which comprises all the

more usual types of this muscle, would be accounted for by these "Reste." In this group the fibres would not necessarily be attached to the modiolus, for "Reste" might remain of any fibres of the pars infra-angularis. If far removed from the modiolus they probably would not be reckoned as risorii. The most striking example of this type of "Rest" is to be recognised in the much debated case described by Froriep (*loc. cit.*), where three layers of muscle are present in the left platysmal region of the face, viz. the crossed platysmal fibres interlacing with the M. caninus, the superficial transverse fibres affixed to the mandible and representing a "Rest" of the noto-platysma, and the deep vertical and labial fibres representing the trachelo-platysma. (*c*) A "Rest" of derivatives of the noto-platysma might be expected in this region, e.g. of the Mm. auriculo-labialis superior and inferior. In the lemurs the M. auriculo-labialis inferior forms the most craniad of the modiolar fibres of the noto-platysma; in them a M. auriculo-labialis superior is also present but widely separated from the former muscle. In the Cercopithecidae the auriculo-labial sheet of fibres have lost their attachment to the ear but are well developed. They are attached to the zygomatic arch and so form a M. zygomaticus. In the orangs there is usually a well-developed auriculo-labialis sheet, which has lost its attachment to the ear, and has no attachment to bone. The cranio-labial group of risorii, i.e. the so-called zygomatic risorii would be accounted for by such "Reste."

Thus it is seen that each of the three groups of risorii above mentioned can be accounted for by a persistence of different platysmal "Reste." Their persistence is encouraged by their attachment to the modiolus, for any muscle having such an attachment must retain some functional value. Also it would be easy to understand the apparent absence of a M. risorius in the Anthropoids and lower Primates.

Orang Z O 1

When first seen after the removal of the skin and panniculus incarnosus there appeared to be a typical and well-marked M. triangularis; all the fibres, however, were from the portio decussata platysmae; a M. transversus menti was not present.

Orang Z O 2

The M. triangularis was a large, fine-fibred, thin subcutaneous sheet of muscle with medial and lateral margins equally well defined. The length of the sheet was 3·8 cm. Average breadth 2·2 cm. and thickness 0·05 cm.

Origin. No fibres were attached to the mandible; the origin was from the fascia of the platysma lateral and inferior to the angle of the mouth, and about the level of the inferior border of the mandible; the distance from the middle line was 3·85 cm. medially and 6·73 cm. laterally.

Insertion. The direction of the muscle fibres was more or less at right angles to those of the platysma. The median fibres ran craniad and medially to reach

the angle of the mouth, and the lateral fibres curled craniad and slightly posteriorly to lie lateral to the M. malaris (B 2). The upper margin of the muscle is in the modiolar area, at the level of a line drawn so as to continue laterally the rimal slit. At its insertion the muscle interlaces with fibres of the M. malaris, M. caninus, M. orbicularis oris and M. buccinator, but there did not appear to be any direct communication with these muscles. The muscle apparently is homologous with the caput latum M. triangularis described for *Homo sapiens*. Crossing superficial and obliquely to the main sheet of the M. triangularis is a small aberrant muscle bundle which ended close to the angle of the mouth.

M. BUCCINATOR (7)

Orang Z O 1

The muscle is a powerful one and, as the inferior fornix mucosae is deeper than the superior, the fibres which arise from the mandible have a greater curl or screw than those from the maxilla. The angle of the mouth was opposite the canine teeth.

Origin. As in man from three areas. (*a*) Maxilla as far medially as the space between the canine and first premolar teeth. (*b*) From the raphe pterygo-mandibularis. (*c*) From the mandible as far medially as the space between the canine and first premolar teeth.

Insertion. From the above origin the fibres stream towards the angle of the mouth in very varying directions; the most anterior are at first almost cephalo-caudal whilst those from the raphe are almost antero-posterior. The insertion may be divided artificially into three layers. The deep layer enters the mucous membrane of the basis modioli; the middle layer interlaces in the modiolar area with the M. orbicularis oris, M. caninus and portio decussata platysmae; the superficial layer of fibres comes wholly from the mandible and interlaces with the fibres of the platysma in the modiolar area but below the angle of the mouth.

Orang Z O 2

In this ape the angle of the mouth was situated opposite the space between the canine and first premolar teeth.

Origin. From the same three areas as Z O 1; from the maxilla as far medially as the first premolar tooth, and from the mandible as far as the space between the canine and first premolar teeth.

Insertion. There is the same diversity of direction for the different sets of fibres as in Z O 1, and the insertion again is described most easily in three layers: (*a*) the deep fibres end in the submucosa of the basis modioli; the intermediate in the modiolar area by interlacing with the M. orbicularis oris, and the superficial also in the modiolar area by interlacing with the M. triangularis and M. malaris. These superficial fibres are derived wholly from the mandibular fibres.

Orang Z O 3

Here the angle of the mouth is opposite the tip of the upper canine tooth; consequently the lower canine alone is visible. The M. buccinator resembles that seen in Z O 1.

Origin. From same three areas; from the maxilla as far medially as the space between the first and second premolar teeth; from the mandible as far as the diastema between the canine and first premolar teeth.

Insertion. This is much the same as in Z O 1 except that a few of the caudal fibres end in the fornix mucosae of the lower lip.

Baboon Z O 4

In this Primate both fornices mucosae are very large but especially the inferior one, which posteriorly becomes a hernia and forms a cheek pouch on either side. The opening of the cheek pouch extends from the posterior margin of the second premolar tooth to the anterior margin of the ramus mandibulae. Owing to the presence of these cheek pouches the M. buccinator presents certain differences to those just described, as it is the one facial muscle to be affected by the presence of these pouches. The angle of the mouth in this primate was opposite the mandibular diastema and both canines were visible.

Origin. The M. buccinator was coarse fibred and took origin from the three usual sources. The fibres from the maxilla and mandible arose as far forwards as the first premolar tooth, but on the mandible there was a large gap in the continuity of the linear origin from the posterior border of the second premolar tooth to the posterior margin of the second molar tooth. The post molar portion of these fibres proceeds caudally and forwards, whilst the premolar fibres run caudally and backwards, and the two sets of fibres meet on the deep surface of the cheek pouch 1·40 cm. from the gingiva. (The tip of this pouch is 4·0 cm. from the gingiva.) Thus there is left on the deep surface of the pouch a triangular area of mucous membrane uncovered by muscle, and lying directly upon the mandible. The remainder of the under surface is covered by these muscle fibres, which sweep around the margin of the pouch to gain and cover the superficial surface completely.

Insertion. The most anterior maxillary fibres run caudo-posteriorly, the fibres from the posterior portion of the maxilla and the raphe run anteriorly, and the mandibular fibres have already been described. All these fibres end in the modiolar area, either in the submucosa or by interweaving with the various muscles in that area. When an uninterrupted view was obtained of the M. buccinator it was noticed that its fibres appeared too long for the cheek, and that this caused a definite infolding or creasing, which divided the muscle along a line parallel with the occlusion of the teeth. This caused an illusion that a raphe ran in an antero-posterior direction through the muscle.

Orang Z O 5

Like the baboon Z O 4 this Primate possesses cheek pouches which are herniae of the buccal mucous membrane. That of the left side alone will be described in detail. The right pouch was much larger than the left, and though the major portion of its superficial surface was covered by muscle fibres some of these were extremely delicate; the remainder of the superficial surface and the whole of the deep surface of the pouch were devoid of muscle covering. The opening of the left cheek pouch extended from the interval between the first and second premolar teeth to the posterior margin of the second molar tooth.

Origin. The M. buccinator had the usual three areas of origin, that from the maxilla extending as far medially as the medial margin of the first premolar tooth, whilst that from the mandible lay wholly posterior to the second molar tooth.

Insertion. The mandibular fibres, and possibly a few from the inferior portion of the pterygomandibular raphe, cover a portion only of the deep-surface of the pouch, and a large area of mucous membrane is devoid of muscle tissue and lies directly upon the mandible. These fibres now wind round the margin of the pouch and completely cover its superficial surface (E 2, E 3). These fibres and those from the raphe and maxilla all proceed towards the modiolar area and angle of the mouth, and end in a fashion not unlike that found in the baboon.

M. ORBICULARIS ORIS (8)

In the five Primates this muscle, though larger, resembled so closely that found in *Homo sapiens* that one general description will suffice, and minor details of each will be given afterwards. As in *Homo* the muscle is not truly orbicular, but is composed of eight elements consisting of the right and left halves of four muscles, viz. the partes marginales superior and inferior, and the partes peripherales superior and inferior. Towards the median plane a section of the lip shows that in each lip, though better marked in the lower than the upper lip, the pars marginalis and pars peripheralis form a continuous sheet of muscle whose cross-section resembles a hockey stick in outline, but this never attains the hook-like formation seen in *Homo*. This means that medially the pars marginalis lies oral and anterior to the pars peripheralis. Laterally and close to the angle of the mouth most of the fibres of the pars marginalis curl around the oral margin of the pars peripheralis to reach its deep surface, where they are inserted into the basis modioli. The pars marginalis inferior, in these Primates, was usually greater than the pars marginalis superior, consequently the number of fibres curling around the pars peripheralis was greater in the lower than in the upper lip. The condition is similar to that found in *Homo*. A few fibres of the pars marginalis in each lip pass superficial to the pars peripheralis and gain insertion into the superficies of the modiolar area. This

condition was met with in the lower lip of *Homo sapiens* (56, 57). The pars peripheralis is a crescentic muscle, being broader and thinner medially and narrower and thicker laterally. The craniad margin of the pars peripheralis superior is thin, whereas that of the pars peripheralis inferior is thicker and rounder. Some fibres of the pars peripheralis superior are attached to the septum mobile nasi and form a well-marked pars nasalis. The M. orbicularis oris covers the origins of the Mm. incisivus superior, labii profundus superior, and pars alaris proprius nasi. The ending of the fibres in the modiolar area is as complicated as that in man, but in Z O 3 a very excellent demonstration of the ending of some of the more superficial fibres is allowed owing to the absence both of a M. triangularis and of fibres from the portio decussata platysmae.

† A list is attached of measurements made of the muscle:

	Z O 1	Z O 2	Z O 3	Z O 4	Z O 5
Pars Marginalis					
Distance from the angle of the mouth to the attachment of the fibres to the basis modioli	0·30	0·35	0·65	—	—
Width of curling fibres at the angle of the mouth					
Superior	0·35	0·05	0·70	0·70	—
Inferior	0·75	0·10	0·70	0·70	—
Pars Peripheralis					
Width of muscle inferior to ala nasi	1·20	2·50	2·05	2·90	
Width of muscle in middle line of the lower lip ...	2·40	3·0	4·0	2·85	—

In Z O 4 the width given of the pars peripheralis superior includes the M. incisivus superior. In Z O 5 a section of the lips did not show any marked angulation between the partes marginalis and peripheralis, otherwise the muscle was similar to that of the other Primates. No measurements were recorded for this Primate.

M. INCISIVUS SUPERIOR (9 A)

In all five Primates the muscle was coarse fibred and well developed. It takes origin in the premaxillary region between the pyriform fossa and the alveoli of the incisor teeth. In the Cercopithecidae the origin lies close to the pyriform fossa, but in the orangs it lies close to the incisor teeth and deep to the fornix mucosae which, for a brief period, separates it from the M. orbicularis oris. Above the fornix there may be a line of cleavage between these two muscles or there may be an interlacement of their fibres, but the fibres of the two muscles always run obliquely to each other. In all five Primates fibres from the M. incisivus pass to the septum mobile nasi. Lateral to the middle line the fibres of the M. incisivus gain the cranial margin of the M. orbicularis oris, and from here to the modiolar area the two muscles run in the same plane and in the same direction and may be inseparable. As the M. orbicularis oris thickens and narrows towards the angle of the mouth the M. incisivus comes to lie anterior to the fornix mucosae, and this position it maintains to its insertion into the modiolar area. This insertion will be described under the modiolar area.

Orang Z O 1

The origin is immediately craniad to the alveoli of the median and lateral incisor teeth, and it extends from the middle line for a distance of 1·58 cm. Opposite the upper canine tooth the thickness of the muscle = 0·12 cm. and its width = 0·55 cm.

Orang Z O 2

The origin is craniad to the alveolus of the median incisor teeth, and stretches from the middle line for a distance of 1·20 cm. Opposite the upper canine the muscle thickness = 0·10 cm. and width = 1·15 cm.

Orang Z O 3

The M. incisivus superior is so closely united to the M. orbicularis oris that it is difficult to separate the two muscles even near the middle line. The origin lies craniad to the medial incisor tooth and extends from the middle line for a distance of 0·75 cm. Opposite the upper canine the width = 1·12 cm.

Baboon Z O 4

The origin in this Primate is closer to the pyriform fossa and further from the incisors than was the condition in the orangs. It extended from the median plane, in the notch between the two median incisors, for a distance of 1·95 cm. The average thickness of the muscle was 0·10 cm.

Macaque Z O 5

It was impossible to separate the M. incisivus superior from the M. orbicularis oris. The origin, like that of Z O 4, lay nearer to the pyriform fossa than the teeth, and extended from the middle line to the medial surface of the canine ridge close to the origin of the M. caninus.

M. INCISIVUS INFERIOR (9 B)

In these five Primates this muscle, though smaller than the M. incisivus superior, is coarse fibred and well developed. Its origin lies deep to the fornix mucosae, and the muscle never lies anterior though it may lie inferior to it. Its relations to the M. orbicularis oris are very different to those of the M. incisivus superior, for the inferior muscle never joins the peripheral edge of the orbicular muscle, but pursues a deeper and more lateral course to be inserted into the basis modioli. At its origin its fibres are more or less intimately interlaced with those of the M. mentalis.

Orang Z O 1

The origin is from the medial surface of the jugum of the canine tooth. The thickness of the muscle is 0·05 cm. and its width is 0·35 cm.

Orang Z O 2

The origin is from the jugum of the lateral incisor tooth and the incisive fossa, and is partially embraced by the fibres of the M. mentalis. The thickness of the muscle is 0·10 cm. and its width is 0·70 cm.

Orang Z O 3

The origin is from the mandible immediately caudad to the central and lateral incisors and the diastema. The thickness of the muscle is 0·08 cm. and its width 1·22 cm.

Baboon Z O 4

The origin is from two areas; the more cephalad is intimately associated with the origin of the M. mentalis, and the more caudad is from the mandible inferior to the M. mentalis. This latter is the larger of the two. These two sets of fibres proceed laterally, the caudad fibres joining the deep surface of those from the more cephalad area of origin. They are all inserted into the basis modioli, some anterior to the neck of the cheek pouch, but the major portion stream across the neck to become attached to its lateral margin (dioptogram D 4).

Macaque Z O 5

Here again the origin is from two areas; the smaller lies lateral and the larger caudad to the M. mentalis. The muscle arising from the latter area measures 0·10 cm. in thickness and 0·70 cm. in width. From these origins the fibres run lateralward to gain the basis modioli in the region of the neck of the cheek pouch (dioptogram E 4).

MODIOLAR AREA

(L. modiolus = nave of a wheel.)

In *Homo sapiens* many of the muscles which surround the rima oris meet, and ultimately interlace with each other lateral to the angle of the mouth. This forms an agger musculosus, so definite, as often to be visible in the living subject, and has been called the "Knoten," "node" and "modiolus." In man this pivoting of the muscular activities upon a hub renders possible the fine precision of movement necessary for the production of speech. In the lower Primates dissected there is less concentration of energy, the interlacing of the various muscles is much less intimate, there is a discus rather than an agger musculosus and the hub of the wheel covers a much larger area; but it remains a hub, with homologous muscle spokes radiating from it. Hence the term modiolar area has been retained in preference to nodal area. The term basis modioli will be used to denote that area of the buccal mucous membrane to which are attached the various modiolar muscles. In the baboon and macaque the neck of the buccal pouch has been considered as part of the basis modioli but, to simplify the diagram, no lines denote its position therein. As in the case

of *Homo sapiens* only a portion of the attachment of the M. buccinator is included in the basis modioli. As the Australian aboriginal is very primitive his basis modioli has been selected for comparison with these Primates. Apart from the contour and size there are other points of resemblance or difference between the modiolus of man and that of the lower Primates, and nothing shows this more graphically than a comparison of the bases modioli. In man and the orangs the muscle insertions are close together and form a compactly arranged plate, whereas in the Cercopithecidae the insertions are scattered in an untidy fashion all over the modiolar area. But the compactly arranged plate of man differs very greatly from that of the orang. In the former the muscle insertions embrace and lie partially medial to the angle of the mouth, whereas in the orang they do not embrace the angle of the mouth but lie wholly lateral to it. But not only is there a marked difference between man and these lower Primates in the method of insertion into the basis modioli of the various muscles, but also there is some difference in the muscles that are inserted. Presently these will be briefly indicated. The modiolar area must vary in shape and size according to the state of activity of the lips and mouth, and the appended measurements denote its resting stage. The base lines for these measurements were obtained by drawing a line to continue laterally the oral slit, and by drawing vertical to this a line passing through the angle of the mouth. The distance from these base lines of the most lateral, most caudad or most craniad points of insertion of a modiolar muscle will indicate the boundaries of the modiolar area. The method of insertion into the modiolar area of the various muscles may be divided into two groups, viz. a deeper layer which gains insertion into the submucosa of the basis modioli, and a more superficial layer which interlaces with the other muscles of this area but has no attachment to the basis modioli. One muscle may send fibres to both these groups. A study of the dioptograms of the norma lateralis and the diagrams of the basis modioli will help to explain the following epitome of the modioli of these Primates.

Orang Z O 1

Dimensions

Lateralad = 3·0 cm.	Caudad = 1·80 cm.
Craniad = 1·50 cm.	Thickness = 0·40 cm.

There is no separation of the layers owing to the close union between the portio decussata platysmae and the M. canino-orbicularis. It will be seen that to the basis modioli are attached not only the Mm. orbicularis oris, buccinator and incisivi, but also the M. malaris and the portiones modiolaris and decussata platysmae. The latter is here labelled (6) as it resembles the M. triangularis. The superficial layer consists of the Mm. malaris and canino-orbicularis and the portiones modiolaris and decussata platysmae. Therefore the Mm. canino-orbicularis and malaris and the portiones modiolaris and decussata platysmae have fibres in both superficial and deep layers.

Orang Z O 2

Dimensions

Lateralad = 2·45 cm.	Caudad = 2·40 cm.
Craniad = 1·90 cm.	Thickness = 0·65 cm.

The deep layer consists of the Mm. incisivi, orbicularis oris and buccinator only. The superficial layer consists of the Mm. malaris, triangularis, canino-orbicularis, and the portio modiolaris platysmae.

Orang Z O 3

Dimensions

Lateralad = 3·80 cm.	Caudad = 2·40 cm.
Craniad = 1·35 cm.	Thickness = not recorded,

The deep layer consists of the M. incisivi, canino-orbicularis, buccinator and the portio modiolaris platysmae. The insertion of the M. incisivus superior lies much more medial and reaches as far as the vertical line through the angle of the mouth. This is an approach to the condition found in *Homo sapiens*. The superficial layer consists of the Mm. canino-orbicularis, buccinator and the portio modiolaris platysmae only.

Baboon Z O 4

Dimensions

Lateralad = 4·4 cm.	Caudad = 2·35 cm.
Craniad = 1·35 cm.	Thickness = 0·70 cm.

The muscle insertions into the basis modioli are very irregular and scattered. The deep layer consists of the following: the M. zygomaticus has a linear insertion which is partially embraced by the fibres of the M. incisivus superior. The M. orbicularis oris has the usual attachment, but that of the M. buccinator is a little unusual owing to the presence of the cheek pouches. The craniad fibres run postero-anteriorly, whilst the caudal or mandibular fibres curl around the pouch and approach the modiolar area somewhat obliquely. The majority of the latter fibres end in the neck of the cheek pouch. The M. incisivus inferior and the portio modiolaris platysmae embrace the neck of the cheek pouch, some fibres being inserted medial and deep, others superolateral to the neck of the pouch. The M. caninus and the deep fibres of the portio decussata platysmae interlace closely with each other immediately superficial to the basis modioli, though they do not gain attachment to the submucosa. This interlacement is a large one and extends through the whole thickness of the modiolar area, so that it is plainly visible on the surface medial and craniad to the thin layer of superficial fibres (dioptogram D 2). The superficial layer consists of the superficial fibres of the portiones modiolaris and decussata platysmae and of the M. incisivus inferior. These are all thin sheets which decussate with each other and with the M. caninus.

Macaque Z O 5

Dimensions

Lateralad = 4·35 cm.	Caudad = 1·45 cm.
Craniad = 0·50 cm.	Thickness = 0·45 cm.

The deep layer. The M. orbicularis oris is inserted in the usual way; the M. buccinator is inserted similarly to that of the baboon Z O 4. The M. incisivus superior and the deep head of the M. zygomaticus are inserted close to one another. The portio modiolaris platysmae and the M. incisivus inferior resemble those of the baboon in as much as they embrace the neck of the cheek pouch, the one insertion being medial and deep and the other supero-lateral to the neck. The lateral insertion of the M. incisivus inferior is a very large one. The M. caninus and portio decussata platysmae again form an extensive though not very intimate decussation. In this Primate some fibres of the M. caninus gain insertion into the basis modioli. The superficial layer consists of the superficial fibres of the muscles just mentioned.

MM. LABIORUM PROFUNDI (10)

The grouping together of the Mm. mentalis and nasalis was suggested by H. Virchow twenty years ago. He says (*Archiv f. Anat. u. Physiol.* 1908, p. 429), "The M. mentalis in its origin as well as in its further relationships, shows an extraordinary resemblance to, if not a complete uniformity with, the M. nasalis; this is the more noteworthy as their genesis has been ascertained." Again the same author states (48), "In man there exists such a far reaching resemblance between the M. nasalis and the M. mentalis, that one might call the M. mentalis the M. nasalis of the lower region of the face, and the M. nasalis the M. mentalis of the middle region of the face." In the present article some departure has been made from Virchow's original conception, and a portion of the M. nasalis is called the M. labii profundus superior, viz. those fibres of the pars alaris M. nasalis which lie medial to the ala nasi. About this portion of the M. nasalis Virchow says (50), "...the fibres ascend perpendicularly craniad and enter the whole of the posterior border of the nares as far as the side of the ala nasi, where they pass imperceptibly into the pars alaris. Therefore I propose to designate this portion as the pars perpendicularis M. nasalis." If the insertion of these fibres was such as described it would not be possible for the pars perpendicularis to function similarly to the M. mentalis. But both macroscopic dissection and microscopic sections show, that this muscle is inserted not into the nares but into the upper lip immediately caudad to the nares. In the orangs the M. labii profundus superior (pars perpendicularis M. nasalis) took origin from the maxilla immediately craniad and lateral to the M. incisivus superior (dioptograms A 7, B 7, C 7). The muscle fibres apparently ascended almost "perpendicularly," but before reaching the nares they became inextricably bound up with the M. orbicularis oris. Careful

dissection failed to show any sign of fibres of the M. labii profundus superior interweaving and passing cranially in company with the fibres of the M. orbicularis oris. On the contrary the attempt to trace these fibres invariably resulted in a free edge of cut muscle fibres. A possible explanation was that the fibres curled anteriorly and passed between those of the M. orbicularis oris, to gain insertion into the skin in a manner reminiscent of the insertion of the labial tractors into the submucosa of the lip; sections were made to test this theory. Unfortunately these were damaged by recently acquired fixatives and lacked detailed definition, but they showed that the hypothesis was correct. Accordingly sections were made from the lip of a European female (figs. 3, 4, 5). Here the fibres of the M. labii profundus superior do not run "perpendicularly" but obliquely craniad and anteriorly, and sweep around the craniad margin of the M. incisivus superior to reach the skin of the upper lip caudad to the margin of the nares. One small slip ends in the skin of the vestibule. The lips, therefore, consist of three layers of muscle; a superficial represented by the labial tractors, an intermediate by the M. orbicularis oris and a deep by the Mm. labiorum profundi. The homology between this muscle and the M. mentalis is better shown if it be compared with the more primitive M. mentalis of the orang Z O 2 than with that of *Homo sapiens*. In this orang there was practically no decussation between the fibres of the opposite sides, much less were any muscle loops formed, there was no enclosed fibrous pad, and no bursa; to reach their insertion into the skin the fibres curled around the inferior margin of the M. orbicularis oris. The action of this type of M. mentalis is to lift orally the medial portion of the M. orbicularis oris together with the loose tissues of the chin, and hence force cranially (orally) the lower lip (figs. 7 and 8). When the M. labii profundus superior is compared with this muscle it is realised how similar they are in position and structure, and how similar must be their function. When acting alone the M. labii profundus superior will drag caudally (orally) the medial portion of the M. orbicularis oris together with the loose tissue inferior to the nares, and depress the lip margin; when acting with the other labial muscles—viz. the M. orbicularis oris and the labial tractors—the lip will be everted owing to the dynamic force of a couple (fig. 6). With regard to the baboon and macaque the M. incisivus superior took origin from the maxilla much nearer to the pyriform fossa than in the orangs; it was not possible to make a satisfactory macroscopic dissection of a M. labii profundus superior and the sections were valueless. The question required further elucidation but no material was available, so the M. incisivus superior alone is shown in the dioptograms of the skull. It was difficult to define the relationship of the septum mobile nasi to the three muscles in this region, viz. the Mm. orbicularis oris, incisivus superior and labii profundus superior. As far as could be ascertained fibres from all three muscles were attached to the septum. The first two muscles might be conceived to use this as a point of origin, but the last must drag the septum caudally as and when it does the skin of the lip. Probably the other two muscles assist in this.

M. LABII PROFUNDUS SUPERIOR (10 A)

Orang Z O 1

The muscle was a single sheet 0·12 cm. thick. Its origin extended from the middle line for a distance of 1·60 cm. laterally.

Orang Z O 2

The muscle consists of two flat sheets each about 0·08 cm. in thickness. The origin of the more caudal extends from the middle line to a point 0·95 cm. laterally, and the other from a point 0·70 cm. to a point 1·62 cm. lateral to the middle line.

Orang Z O 3

The muscle in this ape also consists of two flat sheets. The more superficial lies in the same plane but lateral to the M. incisivus superior, and its origin extends from 0·75 to 1·70 cm. from the middle line. It is inserted into the lip and laterally does not reach the ala nasi. The deeper sheet lies partly deep but chiefly lateral to the superficial sheet. It is likewise inserted into the lip but laterally it is directly continuous with the pars alaris proprius M. nasalis (dioptogram C 4).

M. MENTALIS (M. LABII PROFUNDUS INFERIOR (10 B))

In these Primates the muscle is coarse fibred, powerful, and more primitive in construction than that of *Homo sapiens*; it is more closely akin to the M. labii profundus superior. The origin of the fibres is interwoven with that of the M. incisivus inferior close to the alveoli of the incisor teeth; it is immediately caudad to the gum—i.e. to the mucous membrane which is closely adherent to the periosteum—and therefore lies deep to the fornix mucosae. Some slight crossing of the medial fibres may be present both at their origin and at their insertion, but it is of small moment and, except in the macaque, there is no resemblance to the muscle loops found in *Homo sapiens*. The muscle on each side is fan-shaped medio-laterally, and the medial gap between the two is filled by loose connective tissue which is attached to bone; there is no bursa. The M. mentalis passes deep to the M. orbicularis oris, and some fibres curl around its inferior margin to gain insertion into the skin of the mental area. From this point to the posterior margin of the mental or simian shelf, fibres are passing *en échelon* towards the skin, so the area of insertion is a very large one. To gain insertion into the skin the fibres of the M. mentalis pierce through the M. quadratus labii inferioris and platysma. The action of a muscle such as this is to lift orally the M. orbicularis oris and the loose skin of the mental area, and thus thrust cranially the lower lip.

Orang Z O 1

The muscle takes origin from the alveoli of the incisor teeth and measures 0·75 cm. medio-laterally and 0·50 cm. sagittally. There is a slight interlacement of the fibres of opposite sides both at the origin and the insertion, but the fibres are bowed laterally between these points thus leaving a small medial space. The thickness of the muscle near its origin = 0·10 cm., and its width at the caudal margin of the M. orbicularis oris = 1·40 cm.

Orang Z O 2

The origin was from the alveoli of the incisor teeth and measured 1·30 cm. medio-laterally and 0·55 cm. sagittally. At its origin the muscle was split into two layers by the fibres of the M. incisivus inferior which took origin between them. There was no intercrossing of fibres at their origin and little at their insertion.

Orang Z O 3

The origin is from the alveoli of both incisor teeth and also from that of the canine tooth and from the diastema. It measures 2·68 cm. medio-laterally. There is a slight intercrossing of the fibres of opposite sides both at their origin and insertion and some slight interlacement with the fibres of the M. incisivus inferior.

Baboon Z O 4

The origin was from the alveoli of both incisor teeth and slightly from the canine jugum. Its medial edge was 0·84 cm. distant from the median plane and measured 1·25 cm. medio-laterally and 1·25 cm. sagittally. At its insertion there was slight intercrossing of the fibres of the opposite sides.

Macaque Z O 5

The origin was from the alveoli of the medial and lateral incisors but was 0·30 cm. distant from the middle line. It measured 0·75 cm. medio-laterally. Unlike the other four Primates the muscles of the two sides form a definite loop which encloses a mass of loose fibrous tissue. This was attached to bone and there was no bursa.

M. NASALIS (11)

It is customary to divide this muscle into two portions though according to Virchow it were better to divide it into three, viz. the pars transversa which curls around the ala nasi and ends on the bridge of the nose; the pars alaris proprius which is inserted into the ala nasi, and the pars perpendicularis which is inserted into the inferior margin of the nares. This last has been shown to be inserted into the upper lip and not into the nares, and has been described as the M. labii profundus superior. In none of the Primates dissected was a pars transversa present though in all there was a definite pars alaris proprius. The

origin of this muscle was lateral and often slightly craniad to the M. labii profundus superior or the M. incisivus superior, and lay caudad and even slightly lateral to the ala nasi. The fibres were inserted into the ala nasi where they interlaced freely with the nasal fibres of the M. quadratus labii superioris.

Orang Z O 1

The muscle took origin craniad to the M. labii profundus superior from which it is separated by a definite layer of fascia. The origin is from the medial surface of the canine jugum to a point 0·75 cm. medial to this. The thickness of the muscle is 0·10 cm.

Orang Z O 2

The origin of the muscle is slightly craniad to the M. labii profundus superior and opposite the diastema. At its origin the width of the muscle is 0·50 cm. and its thickness is 0·15 cm.

Orang Z O 3

At its origin this muscle is indistinguishable from the most lateral fibres of the M. labii profundus superior but more cranially it splits off from these to gain insertion into the ala nasi.

Baboon Z O 4

The muscle was pale and fine fibred and took origin cephalad and lateral to the M. incisivus superior. At its origin the muscle was 0·65 cm. in width and 0·10 cm. in thickness.

Macaque Z O 5

The muscle is a delicate slip arising from the maxilla craniad to the M. incisivus superior and 1·10 cm. distant from the median plane.

M. ORBICULARIS OCULI (12)

In these Primates as in man there could be distinguished the three parts into which the muscle has been arbitrarily divided, viz. the partes palpebralis, orbitalis and peripheralis. The *pars palpebralis* showed no peculiarities though the slight exopthalmos present in some of the orangs seemed to increase the area covered by this muscle. The *pars orbitalis* took origin from the medial palpebral ligament and from the orbital margin caudad to this. The fibres thence passed at first caudally and laterally, later cranially, and then medially, thus encircling a large portion of the orbit. These fibres ended in three ways; some ended upon the fascia covering the M. orbito-auricularis, some in the fibro-fatty tissue of the eyebrow, and the remainder passed between the two layers of the M. depressor capitis and intimately interlaced with them. Sometimes it was difficult to demonstrate these two layers of the M. depressor capitis but at other times they were distinct. A peculiar condition existed in the orang Z O 3 and the baboon Z O 4, where laterally there was a definite attachment by strong fibrous tissue of the pars orbitalis to the orbital margin, but

there was no break in the continuity of these fibres. The *pars peripheralis* or *M. malaris* was always well developed, and usually both medial and lateral heads could be distinguished. The medial head sometimes seemed to be in the same plane as the caput angulare M. quadratus labii superioris, but at other times it lay superficial to this muscle; always it lay in the same plane as the pars orbitalis. These fibres ended in the infra-orbital region of the face either medial or superficial to the caput laterale M. malaris. The caput laterale was always well developed and was homologous with a muscle described by Ruge. In his article upon the lemurs Ruge describes and figures a very full development of the M. auriculo-labialis superior which he subdivides into three portions: the M. auriculo-labialis proprius, the M. temporo-labialis and the M. orbito-labialis. A year later in describing the gorilla he further subdivides the last named into M. orbito-labialis and M. orbito-malaris, thus giving a separate entity to the medial fibres of this muscle, which end in the infra-orbital region of the face and do not reach the lip. In the orang Z O 2 there seemed to be a representation of these four portions but the orbito-malaris fibres were very insignificant (dioptogram B 2). In the other four Primates either the temporo-orbital or the auriculo-temporal fibres seem to be present. In all cases the fibres formed the labial tractors for the lateral portion of the upper lip, and medially were closely applied to the labial fibres of the M. quadratus labii superior. Again a peculiar condition existed in the baboon Z O 4, where a short distance below their origin the fibres of the M. malaris were attached by dense fibrous tissue to the malar bone, without any break in the continuity of the muscle fibres. In the present series of dissections this fibrous tether has been met with five times, viz. once in the platysma of the orang Z O 3 where the tethering involved the whole thickness of the muscle and was visible on the surface; once in the pars orbitalis of the orang Z O 3, and three times in the baboon Z O 4 where only the deeper fibres were involved and no evidence of this was visible on the surface of the muscle; a condition similar to the baboon has been mentioned by Ruge also (*loc. cit.*). Such a tethering suggests the initiative by which a muscle ultimately gained true bony attachment. In the macaque and baboon the M. zygomaticus apparently has sprung from auriculo-labial fibres, and a similar condition seems to prevail in the chimpanzee (Virchow) and gorilla (Ruge). In *Homo sapiens* it is difficult to say whether the M. zygomaticus may not have the same genesis and that the origin has shifted medially, but it seems more probable that in *Homo* the genesis is from the temporo- or orbito-labial fibres. The conditions found in the European foetus (57) and the Australian aboriginal (56) support this, and also suggest that the caput zygomaticum and the M. zygomaticus originated from a common muscle sheet. If this were true the tethering of the M. malaris described above would possess some significance.

Orang Z O 1

Some fibres of the pars orbitalis take origin from the medial orbital margin for a distance of 0·12 cm. caudad to the medial palpebral lig., whilst others take origin from the lateral margin of the orbit caudad to the lig. palpebrae laterale, and between the origin of the M. orbito-temporalis and caput infra-orbitale (dioptograms A 7 and A 8). The caput mediale M. malaris lies on the same plane as the caput angulare M. quadratus labii superior but its colour is paler. With this muscle it forms a continuous fan which completely conceals the craniad portion of the caput infra-orbitale, and its fibres end in the infra-orbital region medial to the caput laterale M. malaris. This latter muscle is well developed but its fibres do not run parallel with those of the pars orbitalis. Probably it is derived from the temporo- and auriculo-labialis fibres. It takes origin from the fascia of the M. orbito-temporalis, and is here partially covered by the most craniad fibres of the noto-platysma. It is inserted in two layers, the superficial forming the labial tractors for the lateral portion of the upper lip, whilst the deeper portion passes between the M. caninus and the M. orbicularis oris to be inserted into the basis modioli.

Orang Z O 2

The fibres of the pars orbitalis take origin as far craniad as the origin of the M. depressor capitis and 0·40 cm. caudad to the lig. palpebrae mediale, but it has no origin from the lateral orbital margin. The origin of the caput mediale M. malaris was from a thin fibro-tendinous sheet continuous with the fascia of the M. procerus, from the nasal process of the maxilla, from the lig. palpebrae mediale and from the orbital margin caudad to this. From here the fibres passed caudally and laterally in a screw-like fashion, so that in the infra-orbital region the muscle belly lay at right angles to that of the pars orbitalis (dioptogram B 1). The caput laterale M. malaris comprises auriculo-, temporo- and orbito-labialis fibres, and its origin extends from the pre-auricular fascia over the whole of the temporal region to the pars orbitalis. The fibres end lateral to the angle of the mouth by decussating with the M. triangularis, and medial to this by becoming labial tractors. One insignificant slip ends in the infra-orbital region (M. orbito-malaris).

Orang Z O 3

The whole muscle was paler than usual. The pars orbitalis had the usual origin but extended along the infra-orbital margin for 2·45 cm. from the middle line, overlapping the infra-orbital as well as the angular head of the M. quadratus labii superior. Laterally the deeper fibres of the pars orbitalis are firmly bound to the os zygomaticum by strong fibrous tissue. This attachment is on the anterior surface of the bone lateral to the orbital margin, from the orbital margin and slightly from the medial surface of the orbit. The whole attachment

lies caudad to the palpebral fissure and the lateral palpebral ligament; inferiorly is contiguous with the origin of the caput infra-orbitale. There was no caput mediale M. malaris, and the caput laterale was poorly represented by two feeble and widely separated bands of muscle. The craniad is closely applied to the pars orbitalis, and ends by forming the labial tractors of the lateral portion of the upper lip. The caudad is even more feeble than this and ends beneath the fibro-fatty oral pad, partly by becoming tendinous and partly by intertwining with the M. caninus.

Baboon Z O 4

The pars peripheralis alone requires special mention. The caput mediale is represented by a weak sheet of fibres which end in the infra-orbital region medial to the caput laterale. The caput laterale is a powerful sheet of muscle taking origin in the temporal region immediately lateral to the pars orbitalis, thence passing orally to become the labial tractor of the lateral portion of the upper lip. Caudad to the pars orbitalis the muscle is in close contact with the caput infra-orbitale but is separated from it by a slight increase in the interfascicular fibrous tissue. A few of the most lateral fibres are only 1·5 cm. in length and end in the temporal region. At its origin the muscle is 1·20 cm. in width but as it lies superficial to the M. caninus it is 2·40 cm. in width. The deeper fibres of the caput laterale are firmly bound over a considerable area to the os zygomaticum by dense fibrous tissue, but there is no interruption of the muscle fibres. The superficial fibres are not involved in this tethering, hence there is no evidence of it on the surface of the muscle.

Macaque Z O 5

The pars peripheralis alone requires special mention. The caput mediale is powerful and lies superficial to the caput angulare M. quadratus labii superioris. Its origin is from the orbital margin medial and caudad to the pars orbitalis, and extends for 1·40 cm. caudad to the medial palpebral ligament. The muscle ends in the infra-orbital region superficial to the caput laterale. The caput laterale also is well developed. It takes origin in the temporal region from the fascia of the M. orbito-auricularis, curls around the orbit and proceeds oralwards to become the labial tractor of the lateral portion of the upper lip. Near the margin of the oral pad these fibres lie superficial to the caput angulare and the M. zygomaticus. A few of the most lateral fibres are short and end in the temporal region cephalad to the M. zygomaticus.

M. DEPRESSOR CAPITIS (13)

This muscle was well developed in all five Primates and manifested the peculiarity not described for *Homo* of splitting into two layers. This splitting of the muscle was no artefact, as the adjacent surfaces remained smooth and shiny, and in the case of the macaque Z O 5 between the layers there was a

definite amount of dense areolar tissue in which the angular vein was seen for a short part of its course. The terminal fibres of the pars orbitalis M. orbicularis oculi passed between the two layers of the M. depressor capitis, and ended by intertwining with one or both, thus uniting them laterally. In the caudal portion of the muscle the two layers were often inseparable, and only in the cephalad portion was a line of cleavage existing between them. This splitting of a muscle into layers has been met with in the M. profundus superior of the orang Z O 2, in the noto-platysma at the nape of the neck and the muscles in the occipital region of the baboon Z O 4, and macaque Z O 5. The panniculus incarnosus of the orang was remarkable for the ease with which it could be split into layers, so some common cause may underlie these findings. The muscle took origin from the orbital margin craniad to the lig. palpebrae mediale, and the fibres spread out fanwise to end in an area extending from the glabella to the middle of the eyebrow region. (In these Primates there were no eyebrows such as are associated with *Homo sapiens*, but beneath the skin there was the same fibro-fatty layer of the panniculus incarnosus.) Craniad to its origin the muscle often came into such close relationship with the M. procerus that it was not possible to separate the fibres of the two muscles.

Orang Z O 1

In this Primate the muscle splits into three layers. The superficial layer, separable throughout its whole length from the remainder of the muscle, takes origin from the orbital margin immediately craniad to the M. orbicularis oculi, and spreads out fanwise towards the usual insertion into the fibro-fatty panniculus of the glabella eyebrow region, extending from 0·3 to 2·30 cm. from the middle line. It is with this layer that the terminal portion of the pars orbitalis interdigitates. A few of its fibres join both the caput angulare M. quadratus labii superioris and the caput mediale M. malaris (dioptogram A 1; in the inset this portion of the muscle is reflected laterally together with the M. orbicularis oculi). Caudad to the M. corrugator the intermediate and deep layers are bound inextricably together, and the superficial surface of this common muscle sheet is joined by the M. procerus and some fibres of the caput angulare. Thus there is formed a very complex muscle mass in which ends the infra-orbital branch of the facial nerve, after it has crossed superficial and craniad to the lig. palpebrae mediale. The common origin for the intermediate and deep layers is from the orbital margin craniad to the superficial layer, from the nasal process of the maxilla and nasal bone medial to this; the whole origin covers a horizontal linear area (dioptogram A 7). As the common muscle mass passes superficial to the M. corrugator it splits medially into two layers, which are united laterally by the fibres of the M. corrugator passing through them to its insertion. Craniad to the M. corrugator the two layers are quite distinct from each other. The intermediate layer, with which is combined the M. procerus, could not be separated from the M. frontalis, but it was not to be determined whether this was due to a direct continuity or to an intimate

interlacement of the fibres of these muscles (Huber(28)). The deep layer gains a crescentic line of attachment to the galea aponeurotica, the highest point of which is 1·90 cm. craniad to the glabella (dioptogram A 1, dotted line in inset).

Orang Z O 2

In this Primate two layers can be distinguished but not so distinctly as the layers of the orang Z O 1. The origin of the muscle is from the orbital margin and inner wall of the orbit, and the insertion is as usually described. The terminal fibres of the pars orbitalis end between the two layers and interlace with both, thus lessening the separation of the layers even craniad to the M. corrugator. At its origin the M. depressor capitis is closely applied laterally to the M. orbicularis oculi and medially to the M. procerus; above its origin it is not possible to separate the M. depressor capitis from the M. procerus.

Orang Z O 3

The muscle is well developed, and though there is no splitting into layers the fibres of the pars orbitalis seem to end between the superficial and deep surfaces of the muscle; the deep fibres of the muscle are more or less intimately connected with the M. corrugator. On the left side a few superficial medial fibres of the M. frontalis join those of the M. depressor capitis, which in its turn sends a few superficial fibres to join the caput angulare M. quadratus labii superioris. The origin is from the orbital margin immediately above that of the M. orbicularis oculi, and the insertion is into the glabella eyebrow region extending from the middle line to 2·70 cm. lateral to this. In the middle line there is a light decussation of the fibres of the muscles of the opposite sides.

Baboon Z O 4

The muscle is well developed, and near its insertion splits into two layers which enclose the terminal fibres of the pars orbitalis. The muscle is fan-shaped taking origin from a narrow area of the orbital process of the frontal bone and being inserted into the glabella eyebrow region, from the middle line and for a distance of 2·0 cm. lateral to this. Laterally its fibres are intermingled with those of the subjacent M. corrugator as it proceeds to its insertion.

Orang Z O 5

The muscle, which is large and well developed, takes origin from the orbital margin craniad to the M. orbicularis oculi. It is fan-shaped and separated into two layers by some dense fibrous tissue, in which the angular vein runs for a short distance. The superficial layer gains the median plane half way between its origin and the glabella, and ends in the fibro-fatty panniculus of the glabella eyebrow region where it interlaces freely with the caput angulare, M. frontalis and the pars orbitalis. The deeper sheet lies deep to the above and, passing superficial to and partly intermingled with the M. corrugator, ends in the galea deep to the glabella eyebrow region.

M. CORRUGATOR (14)

In these Primates the muscle, which lay deep to the M. depressor capitis, was more powerfully developed and had a more extensive origin than that of man. This origin embraced the medial angular process of the frontal bone and sometimes the nasal bone. It extended from the glabella to the fronto-maxillary suture, and from the orbital margin to within 0·05 to 0·25 cm. of the median plane. It approached nearest the median plane immediately caudad and to the glabella. Its more craniad fibres, which resemble the M. corrugator of *Homo sapiens*, took a wide origin between the glabella and the orbital margin, and thence ran obliquely lateralad to gain insertion into the eyebrow region. The more caudad fibres are not represented in *Homo sapiens*; these took origin from the orbital margin cephalad to the M. depressor capitis, and from the medial angular process of the frontal bone as far as the infra-glabellar region. Thence the fibres coursed cranially until in contact with the more horizontal cephalad fibres, when they curved laterally to gain insertion into the eyebrow region. The lateral insertion of this muscle was difficult to estimate but it seemed to extend across the orbit. These caudad fibres ran in a direction similar to the lateral fibres of the M. depressor capitis, and there was usually an interchange or decussation of the fibres of these muscles. But, apart from this, to reach their insertion the fibres of the M. corrugator always passed through the deep, and sometimes through the superficial layer of the lateral portion of the M. depressor capitis. In the eyebrow region it pierced the M. orbicularis oculi to gain the fibro-fatty panniculus. The average thickness of the muscle was 0·11 cm.

Orang Z O 1

The muscle took origin from the median angular process of the frontal bone and from the nasal bone, and approached to within 0·05 cm. of the median plane or may have reached it. The muscle was 0·08 cm. in thickness, and the most median point of its insertion into the eyebrow was 2·20 cm. lateral to the glabella.

Orang Z O 2

The muscle was closely intertwined with the overlying M. depressor capitis and difficult to separate from it. The origin did not involve the nasal bone but approached to within 0·25 cm. of the middle line. The muscle was 0·14 cm. thick and 1·0 cm. broad. The most median point of its insertion was 2·20 cm. lateral to the glabella.

Orang Z O 3

The thickness of this muscle was 1·20 cm.

Baboon Z O 4

The origin of this muscle reached to within 0·10 cm. of the middle line. It was 1·20 cm. in breadth. The most median point of its insertion was 1·30 cm. lateral to the glabella.

Macaque Z O 5

In this Primate, more than in the others, the muscle resembled that of *Homo sapiens*, since the caudad fibres ran obliquely lateral rather than cephalad. Its most median point of insertion was 1·40 cm. lateral to the glabella.

M. PROCERUS (15)

As the activities of the facial muscles are but imperfectly understood, it is doubtful whether the term M. depressor glabellae, suggested by H. Virchow, is comprehensive enough for this sagittal muscle. For the five Primates under discussion the term M. procerus is admirably descriptive, as the muscle, at best, is but a slender band; at times it is absent. Cranially it is continuous or intimately interlaced with the M. frontalis, and in addition has some intercommunication with the M. depressor glabellae and the caput angulare. Caudally it takes origin from the fibro-cartilaginous area of the nose or from the bone immediately craniad to the pyriform fossa.

Orang Z O 1

The muscle is 0·02 cm. thick and 0·36 cm. wide. Below the glabella it fuses with the middle layer of the M. depressor capitis (q.v.), and this combined sheet is apparently continuous with the M. frontalis. Caudally it partly overlies the caput angulare from which it is easily separated; it takes origin from the fibro-cartilaginous area of the nose.

Orang Z O 2

The muscle is paler in colour than the caput angulare and easily distinguished from it, but is of the same colour as the M. frontalis with which, apparently, it is continuous. The muscle is triangular in shape, being broadest in the region of the glabella and pointed at its origin from the fascia and bone above the fossa pyriformis.

Orang Z O 3

The muscle is absent.

Baboon Z O 4

The muscle is extremely slender, being only 0·035 cm. thick and 0·45 cm. wide. In the region of the glabella it is difficult to trace so narrow a muscle through the dense connective tissue, but its fibres apparently blend with those of the M. frontalis. A few fibres are attached to the region of the naso-frontal suture. It takes origin from the fibro-cartilaginous area of the nose.

Macaque Z O 5

In this Primate no line of cleavage existed between this muscle and the caput angulare. In the region of the glabella these fibres were inseparably intermingled with the superficial fibres of the M. depressor capitis and with the M. frontalis; caudally they take origin from the fibro-cartilaginous portion of the nose.

M. EPICRANIUS

This consists of four flat muscle sheets—two frontal, the orbito-auricular, and two occipital, the auriculo-occipital—which are connected over the cranial dome by a strong sheet of fascia, the galea (aponeurotica).

M. ORBITO-AURICULARIS (16)

This muscle consists of two portions, a superficial (M. frontalis) and a deep (M. orbito-temporalis).

The baboon Z O 4 and the macaque Z O 5 are alike in the arrangement of the musculature of the cranial dome, and in them this arrangement of the muscles is patent. The findings in the orang Z O 3, and to a less extent in the orang Z O 2, indicate for the orangs a similar composition of the large and apparently single layered sheet of muscle.

(*a*) *M. frontalis.* The muscle was not powerful but extended high up the cranial dome, and in one case interlaced with the M. occipitalis in the median plane. The muscles of each side met in the median plane, and the median fibres were apparently continuous with those of the M. procerus. The lateral fibres were inseparable posteriorly from the median fibres of the M. orbito-temporalis, but at the eyebrow region they lay superficial to this latter muscle. The muscle had no attachment to bone, but took origin from the galea of the vertex and was inserted into the fibro-fatty panniculus of the eyebrow region, where it interlaced with the other muscles present.

Orang Z O 1

The M. frontalis and the M. orbito-temporalis apparently lay in the same plane and could not be separated. In the median plane at the vertex some fibres of the M. frontalis interdigitated with the M. occipitalis[1], and at the glabella they were inseparably interlaced with or formed part of the middle layer of the M. depressor capitis, with which the M. procerus was united. Lateral to this in the eyebrow region the fibres passed deep to the M. orbicularis oculi and gained attachment to bone; this is quite at variance with the findings in the other Primates.

Orang Z O 2

This muscle is less extensive than in the orang Z O 1 and is pale in colour. Laterally the fibres pass superficial to the tendinous origin of the M. orbito-temporalis.

Orang Z O 3

The muscle was pale in colour. Medially its thickness was 0·08 cm. but laterally it faded away to a very thin sheet, which lay superficial to the M. orbito-temporalis over the greater part of its insertion and craniad to this. As there is no M. procerus the ending of the medial fibres is different to the general

[1] This was confirmed histologically.

description. On the left side they end by joining the deep surface of the M. depressor capitis; on the right side they do this also but, in addition, some fibres pass deep to this and end in the median plane of the nose, in series with the fibres of the caput angulare of the same side but superficial to those of the caput angulare of the opposite side.

Baboon Z O 4

The muscle is thin, being 0·04 cm. in thickness and dark in colour. The fibres are inserted into the eyebrow region where they lie superficial to the M. orbito-temporalis; the origin of the lateral fibres is from the cartilage of the ear, i.e. from the eminentiae scaphae and triangularis in company with the M. auricularis superior, and from the ascending portion of the helix in company with some fibres of the M. orbito-temporalis.

Macaque Z O 5

The origin was destroyed by the operation of trepanning. Its median fibres interlaced with the superficial layer of the M. depressor capitis and the M. procerus; its lateral fibres ended in the eyebrow region superficial to the origin of the M. orbito-temporalis.

(*b*) *M. orbito-temporalis* (orbito-auricularis proprius). In all the Primates this muscle was well developed and fan-shaped. In the orangs the caudad fibres, which were almost vertical, were darker in colour, shorter and thicker, whilst the craniad fibres, which ran almost horizontally, were paler in colour, longer and thinner. The tendinous origin of the muscle was from the arcus superciliaris, deep to the M. frontalis, and from the lateral angular process of the frontal bone; all but the most lateral of the latter fibres also were covered by the M. frontalis. The insertion of the muscle was a very extensive one. The most craniad fibres, which lay in the same plane and were inseparable from the M. frontalis, were inserted into the helix of the ear or ended anterior to or upon the fascia of the M. auricularis superior; the intermediate fibres were inserted into the fascia anterior to the external ear and into the cartilaginous external auditory meatus. The caudad fibres—present only in the orangs—which lay deep to the M. malaris and pars orbitalis M. orbicularis oculi—ended on the temporal fascia stretching as far down as the zygoma.

Orang Z O 1

The origin was from the lateral half of the superciliary ridge and from the lateral angular process. The colour and thickness of the muscle appeared the same in all regions.

Orang Z O 2

The muscle fibres were coarser than those of the M. frontalis. The extent of the origin from the superciliary ridge was not recorded.

Orang Z O 3

In this orang the demarcation between the M. frontalis and the M. orbito-temporalis was better than in the previous Primates, and resembled the conditions found in the baboon Z O 4. The origin was from the lateral angular process, and the superciliary ridge as far medially as and partially underlying the origin of the M. corrugator. The insertion was into the galea anterior to the M. auricularis superior, the spina helicis, the cartilaginous external auditory meatus and an irregular area of the temporal fascia.

Baboon Z O 4

The origin was from the lateral angular process, and the superciliary ridge to within 1·0 cm. of the middle line. The most lateral fibres were not covered by the M. frontalis but ran in the same direction, and at first sight might have been mistaken for them. The insertion was into the anterior and outer surface of the helix and the fascia anterior to the ear. No fibres stretched caudally towards the zygoma.

Macaque Z O 5

The muscle was more powerful and coarser fibred than the M. frontalis. The origin was from the lateral angular process, and the superciliary ridge to within 1·40 cm. of the middle line. The insertion was by muscle fibres into the galea anterior to the M. auricularis superior, to the anterior and outer surface of the helix, and by tendinous fibres into the fascia anterior to the ear. No fibres stretched caudally towards the zygoma.

M. AURICULO-OCCIPITALIS (17)

This embraces the occipital epicranial musculature. In the occipital region there are two sheets or layers of muscle, a superficial, the M. cervico-auriculo-occipitalis, and a deep, consisting of the M. occipitalis and the posterior extrinsic auricular muscles. The Cercopithecidae show a complete and primitive development of this region. In both those dissected, but especially in the larger—baboon Z O 4—could be seen clearly the relations of the different layers of the nape region of the noto-platysma to the fascia and muscles of the occipital epicranial region, since the three layers of the noto-platysma and their corresponding fasciae were well developed and distinct. In the baboon Z O 4 the attachment to the ligamentum nuchae of the superficial layer of the noto-platysma is still by strong muscle fibres, but in the macaque Z O 5 it is by a tendinous or fascial sheet. In both these Primates this superficial layer of the noto-platysma is continuous in the occipital epicranial region with a layer of strong fascia, which extends as a separate superficial layer as far as the insertion into the galea of the M. occipitalis. The middle layer of the noto-platysma in both these Primates still persists as the M. cervico-auriculo-occipitalis. The superficial and deep perimysia of this latter muscle unite on its cranio-medial

aspect to form a sheet of fascia, separate and distinct from the superficial layer already mentioned but joining it at the insertion of the M. occipitalis. The deep layer of the noto-platysma does not reach as far as the nuchal line being 0·50 cm. caudad to it. In the space between the craniad margin of the deep layer of noto-platysma and the medial line can be seen dimly the oblique fibres of the M. trapezius, which extends as a muscular sheet up to the nuchal line in the middle line of the neck. The perimysium of the deep layer of the noto-platysma is directly continuous with a layer of thick fascia which covers this upper portion of the M. trapezius, and this fascia is contiguous cranially with the perimysium of the M. occipitalis. Therefore it would appear that the deep layer of the noto-platysma and the M. occipitalis are on the same morphological plane; and as the M. auricularis posterior is on the same morphological plane as the M. occipitalis, it must be in the same morphological plane as the deep layer of the noto-platysma. The M. occipitalis is inserted into the cranial aponeurosis along the same line whereat it is joined by the sheets of fascia representing the two superficial layers of the noto-platysma (see dioptograms D 5 and D 6). The conditions found in the macaque Z O 5 were so nearly identical with those of the baboon Z O 4 that no special dioptograms were necessary. Unfortunately Ruge regarded the Primates possessing cheek pouches as an isolated group outside the main ancestral stem, but his dissection and figure of a Cynocephalid (41) resembles the above. Ruge (Halbaffen, pp. 267–268) says the M. auriculo-occipitalis was merely a portion of the noto-platysma which became independent owing to the degeneration of the nuchal fibres of the platysma; that this split into two layers a superficial or occipital portion which had lost its origin from the middle line, and an auricular or deep portion which gained possession of the main origin from the lig. nuchae. Again the same author (*Primaten*, p. 45) states that the M. occipitalis of man corresponds to the M. auriculo-occipitalis of the Primates, and is therefore a superficial muscle but it has lost completely its nuchal fibres. The present dissection supports but modifies this view, as it regards the M. occipitalis as a deep and not a superficial layer of muscle, and as being on the same plane as the posterior auricular muscles.

In the orang the M. auriculo-occipitalis proprius apparently consisted of a single sheet of muscle, as no line of cleavage or overlapping of fibres could be found. This sheet was probably formed by the fusion of the occipital and posterior auricular muscles, and in that case would be derived from the deep layer of the platysma, to the exclusion of the middle and superficial layers which would be represented by fasciae. The arguments in favour of this are: that the method of insertion of the fibres into the cartilage of the ear resembles that of the M. auricularis posterior rather than that of the M. cervico-auriculo-occipitalis; that in the orang Z O 1 the caudal edge of the muscle was continuous with a thin sheet of muscle lying upon the M. trapezius, and in the same plane as its perimysium (dioptogram A 2). This sheet of muscle could only be a "Rest" of the deep layer of the noto-platysma; and that in a hybrid

black lemur[1] there were present in the nape of the neck and occipital regions three layers of muscle and fascia similar to those of the macaque. But in this lemur the deep occipital epicranial layer formed a fan, consisting of a large M. occipitalis which medially reached the middle line and laterally closely adjoined the three slightly divergent posterior auricular muscles. The most caudad of these ran horizontally, and the resemblance of this deep occipital epicranial layer to the M. auriculo-occipitalis proprius of the orang was unmistakable. From the foregoing observations and from the references consulted it seems that the superficial layer of the noto-platysma does not become a cranial muscle, but is represented by a layer of fascia; that the middle layer of the noto-platysma may persist in many of the lower Primates, e.g. baboon, macaque, lemur and in other mammals, e.g. dog, as the M. cervico-auriculo-occipitalis—in the former it is a partial, in the latter a complete investment for the occipital epicranial region; that in the higher Primates and man both these superficial layers of the noto-platysma disappear or are represented by fascia, and the deepest layer alone remains as the M. occipitalis and the posterior auricular muscles. In the orangs this forms a complete investment for the occipital epicranial region as the M. auriculo-occipitalis proprius, but in *Homo sapiens* the constituent muscles are separated.

(*a*) *M. cervico-auriculo-occipitalis.* This muscle was present in the baboon Z O 4 and macaque Z O 5 but not in the orangs.

Baboon Z O 4

The semi-tendinous origin of this muscle is not from bone, but from the lig. nuchae between the origins of the two other layers of the noto-platysma, for a distance of 4·7 cm. from the inion. Caudally its fibres of origin are closely interwoven with those of the deep layer of the noto-platysma, but for the greater part they are quite separate. The muscle is 0·10 cm. thick and 2·9 cm. wide. Its fibres run craniad and laterally until they reach the M. auricularis superior, when the majority of the fibres split to enclose the posterior margin of the muscle but passing deep rather than superficial to it. Laterally there are two other modes of insertion; some fibres are inserted into the eminentia conchae of the cartilage of the ear in conjunction with a band from the superficial layer of the noto-platysma; a larger bundle crosses superficial to the M. auricularis superior at the root of the ear and ends on the fascia of the M. orbito-temporalis.

Macaque Z O 5

The muscle takes origin from the external occipital protuberance (planum occipitale), and from the lig. nuchae between the superficial and deep layers of the noto-platysma. The fibres proceed cranially and laterally, and end by splitting to enclose the posterior margin of the M. auricularis superior, and by insertion into the eminentia triangularis of the ear cartilage.

[1] At present under dissection. This head was obtained through the courtesy of Professor J. P. Hill, University College, London, and Dr Scott, Zoological Gardens, London.

(*b*) *M. occipitalis.* As a separate muscle this was not present in the orangs.

Baboon Z O 4. (Dioptogram D 6 and inset)

The muscle lies deep to and is partially covered by the M. cervico-auriculo-occipitalis. Its most lateral fibres form a band of muscle somewhat superficial to and distinct from the main body of the muscle. This band is 0·65 cm. wide and 0·13 cm. thick and takes origin from the planum occipitale; proceeding at first almost horizontally and laterally it crosses and conceals the origin of many of the fibres of the deeper layer. After this the band becomes more sagittal in direction and proceeds parallel to, and is inseparable from, the remainder of the muscle. It is inserted with the main sheet into the cranial aponeurosis. This band would seem to be a "Rest" of the nuchal portion of the deep layer of the platysma. Its perimysium is continuous with that covering the deeper portion of the M. occipitalis, and through it with the deepest of the three layers of fascia present in this region. The remainder and main portion of the M. occipitalis takes origin immediately lateral to the planum occipitale, from a protuberance of the occipital bone which extends lateral to the inion and above the superior nuchal line. The origin consists of a sagittal and an horizontal portion. The sagittal portion lies 1 mm. from the median plane and the horizontal extends laterally for 1·33 cm. From here the fibres run sagitto-laterally to end in the superficial layer of the galea (q.v.) in a coronal plane opposite to the anterior margin of the aural cartilage. The three layers of aponeurosis in the occipital region fuse also in this plane. The lateral fibres of this layer of the M. occipitalis join the deeper surface of the superficial layer. At the caudad edge of the posterior auricular muscles the M. occipitalis is 1·30 cm. wide and 0·20 cm. thick, whereas at its insertion it is 2·32 cm. wide and 0·10 cm. thick.

Macaque Z O 5

The muscle lies deep to and is partially covered by the M. cervico-auriculo-occipitalis. It is well developed and takes origin from the planun occipitale and a small area of the superior nuchal line lateral to this. The fibres spread out fanwise to be inserted into the galea. The muscles of the two sides are in contact throughout.

(*c*) *M. auriculo-occipitalis proprius.* This muscle is present in the orangs but not in the other two Primates; it covers completely the back of the head. It is a large fan-shaped muscle sheet taking origin from the planum occipitale and the superior nuchal line, and being inserted into the eminentia conchae of the cartilage of the ear and the galea of the scalp posterior and medial to the M. auricularis superior. The medial fibres run sagittally and the lateral fibres horizontally.

Orang Z O 1

The medial fibres of this muscle are in contact throughout and a few interlace at the vertex with those of the M. frontalis. The fibres inserted into the cartilage of the ear are muscular throughout. The origin of the muscle extends

for 3·10 cm. from the middle line. A peculiar fan-shaped sheet of fibres less powerful than those already described arose from the fascia covering the Mm. sterno mastoid and trapezius. These lie caudad to the main muscle but are inserted with them into the ear cartilage (dioptogram A 2).

Orang Z O 2

The fibres passing towards the ear end in a thickening of the fascia which almost amounts to a tendon, and are thereby attached to the eminentiae conchae.

Orang Z O 3

The muscle is pale and not so well developed. Its origin does not reach the middle line but extends from 0·27 to 5·30 cm. from the middle line. The medial fibres of the two sides come in contact with each other 3·50 cm. craniad to the inion. The insertion into the ear cartilage is muscular throughout and is divided into two slips.

GALEA (18)

Orang Z O 3

The conditions found in this Primate may be taken as representative for the orangs. The galea was thick and well developed and composed of a single layer. Anteriorly it is attached to the glabella, the orbital ridges and the processus fronto-sphenoidalis of the os zygomaticum; posteriorly it is attached to the superior nuchal line, to a ridge in continuity with this across the mastoid process, and to the bony external auditory meatus; laterally it is very thin and passes superficial to the temporal fascia to gain attachment to the zygomatic arch.

Baboon Z O 4

In this Primate the galea was a complex one consisting of two distinct layers, and separated from the periosteum by a large bursa.

The superficial layer. At the vertex cranii situated between the anterior, lateral, and posterior cranial muscles is a small aponeurotic area measuring 1·80 cm. sagittally and 3·10 cm. medially. To it are attached all the muscles that run towards the vertex; at the insertion of the M. occipitalis this layer receives or splits into the three layers that are continuous with the corresponding layers of the noto-platysma. This layer may be said to cover the whole superficial surface of the occipital region. At the vertex and elsewhere this superficial layer is separated from the deep by a little loose areolar tissue.

Deep layer. Anteriorly this is very thick (0·09 cm.) but posteriorly it is very thin (0·03 cm.); this difference in thickness may be due to the mode of death causing oedema of the anterior portion. Anteriorly for a distance of 3·0 cm. from the glabella, and posteriorly for a distance of 1·20 cm. from the inion, the deep layer is closely bound to the periosteum; laterally it is bound to the temporal fascia though the union here is not so intimate. Between this deep

layer of the galea and the periosteum in the region of the vertex there exists a large bursa measuring 10·0 cm. sagittally and 8·0 cm. coronally. Sections showed that this bursa was lined by meso-epithelium which gave to the surface a shiny appearance. When this layer of the galea is detached from the periosteum and temporal fascia its attachments were as follows: anteriorly to the glabella, the origin of the M. corrugator, the supraciliary ridge, and the origin of the M. orbito-temporalis; laterally it passed to the zygoma and the fascia of the parotid; posteriorly to the bony external auditory meatus, the superior nuchal line, the origins of the Mm. auricularis posterior and occipitalis and the inion.

Macaque Z O 5

Owing to the scalp injury the medial portion of the galea could not be investigated. Its lateral attachments resembled very closely those of the deep layer of the galea in the baboon Z O 4.

M. AURICULARES EXTRINSECI (19)

The M. auricularis superior is present in all the Primates dissected, but the M. auricularis posterior is present as a separate muscle only in the baboon and macaque. The M. auricularis anterior does not exist as such in any of the five Primates though some fibres of the Mm. auricularis superior, frontalis and orbito-auricularis may function as such.

(*b*) *M. auricularis superior.* In the orangs this is a leaf-shaped thin sheet of muscle running in a coronal direction between the Mm. frontalis and auriculo-occipitalis proprius. It takes origin from the galea near the vertex and has a musculo-tendinous insertion into the eminentia conchae of the ear-cartilage. In the orang Z O 3 there is some intermingling with the fibres of the M. orbito-temporalis.

Baboon Z O 4 and **Macaque Z O 5**

This is a thin sheet of muscle which runs in a coronal direction and takes origin from the galea but further from the vertex than in the orangs. The posterior margin of the muscle is obscured by the overlapping fibres of the M. cervico-auriculo-occipitalis, and the anterior margin is inseparable from the fibres of the M. frontalis which are attached to the ear cartilage. The muscle is inserted into the eminentiae scaphae and triangularis of the cartilage of the ear.

(*a*) *M. auricularis posterior.*

Baboon Z O 4

(Dioptogram D 6 and inset.) In this Primate there are in this region two muscles in close apposition. The direction of their fibres is parallel to the craniad margin of the deep layer of the noto-platysma, they are muscular throughout and are inserted into the eminentia conchae of the ear cartilage.

The more cephalad muscle takes origin lateral and inferior to the M. occipitalis but from the same occipital protuberance; the more caudad takes origin from the planum occipitale, the occipital protuberance and the superior nuchal line. Lying deep to this more caudad muscle is a thin, weak band of muscle bifurcated at its lateral extremity.

Macaque Z O 5

The origin of this muscle is thin and chiefly tendinous from the superior nuchal line lateral to the origin of the M. occipitalis. It is inserted by two muscle bellies into the eminentia conchae of the ear cartilage.

MM. VARII ET DIVERSI (20)

M. anomalus maxillae (?). In the orang Z O 1 lying immediately lateral to the origin of the M. caninus, and extending from the canine fossa to the malar eminence, are some transverse fibres which lie closely approximated to the bone throughout (dioptograms A 7 and A 8). The position is an unusual one and the fibres probably are derived from the same anlage as the M. caninus.

SUMMARY

The amount of variation in the facial muscles of the orangs is greater than anticipated, though such variations usually do not interfere with the structural plan of the facial musculature, which is the same for all five Primates as for *Homo sapiens*; the only point of real difference is the presence in the Primates of the large noto-platysma. This muscle, which is the only type of platysma present in the subprimate mammalia, in the Primates is being replaced gradually by a new muscle, the trachelo-platysma. This may be connected with the assumption of the upright position. In the Cercopithecidae both muscles are very large and nearly equal in size. In *Homo sapiens* the trachelo-platysma has completely ousted the noto-platysma, and remains as the standard platysma for this family. It is curious how closely, apparently, this replacement of the noto-platysma by the trachelo-platysma corresponds to the evolutionary grouping of the Primatae. As the Cercopithecidae are lavishly endowed with facial muscles, and as no support was found for the statement that their facial musculature was materially altered by their possessing buccal herniae or cheek pouches, they probably would be a much better standard for the facial musculature of the Primatae than the Lemuroidae.

The labial tractors showed considerable variation. No caput zygomaticum was found in any of the five Primates. In the orangs the tractors resembled otherwise those of *Homo sapiens*. In the Cercopithecidae there was no M. quadratus labii inferioris, and in the upper lip either the caput angulare or the caput infra-orbitale may be absent. The tractors for the lateral part of the upper lip are supplied by the M. malaris, reinforced by fibres from the M.

zygomaticus when this is present. No M. zygomaticus is present in the orangs, and in the other two Primates it is derived from the auriculo-labial, and not from the temporo-labial fibres, as apparently is the case in man. It has been shown that in laughter the M. caninus is not in a state of activity, but that the caput longum M. triangularis is in a state of violent activity. As it is physiologically impossible for one half of a muscle fibre to be quiescent whilst the other remains in a state of activity, the above observation would seem to disprove the theory that the M. triangularis is a caudad extension of the M. caninus. From the present dissection it would appear that it is derived from the portio decussata of the trachelo-platysma. These fibres interlace in the modiolar area with the M. caninus; the interlacement may be so slight as to be readily seen, or so intimate that it is not possible to distinguish or separate their respective fibres. Also it is shown that some spurious types of the M. risorius may be derived from the portio decussata of the trachelo-platysma but that, in all probability, the majority of these variable muscles are derived from "Reste" of the noto-platysma.

The modiolus of man consists of an agger musculosus wherein the muscular activities are concentrated around and medial to the angle of the mouth; the modiolar area of the Cercopithecidae exhibits lack of concentration; it consists of a discus musculosus wherein the muscle insertions are scattered lateral to the angle of the mouth, and often are widely separated from each other. The modiolar area of the orangs lies midway between these two states.

A pars transversa M. nasalis could not be found in any of the five Primates, and the so-called pars alaris M. nasalis consists of two groups of muscle fibres, which at times are separated by a thin fascial plane. The results of the activities of these two groups is so different that they have been described as separate muscles. The lateral portion acts upon the ala nasi and may be called the pars alaris proprius; the medial (pars perpendicularis of Virchow) does not act upon the inferior margin of the nares as is usually described, but upon the upper lip immediately caudad to the nares, and may be called the M. labii profundus superior. This muscle resembles so closely the primitive M. mentalis found in the Cercopithecidae, that the two have been classed together as the Mm. labiorum profundi, in contrast to the two quadrate muscles which have been called the Mm. labiorum superficiales. The M. depressor capitis usually splits into two layers between which end the fibres of the pars orbitalis M. orbicularis oculi; the M. corrugator in these Primates is found to be larger and more powerful than that of *Homo sapiens*. The M. orbito-temporalis is a large fan-shaped sheet of muscle, whose origin from the lateral angular process and the major portion of the superciliary ridge lies deep to the M. frontalis. Finally in some Subprimates and lower Primates the middle layer of the noto-platysma still persists as the M. cervico-auriculo-occipitalis, and forms the superficial musculature of the occipital region. The true M. occipitalis represents the deep layer of the noto-platysma, and in the higher Primates and man seems the only layer of muscle present in the occipital region.

In conclusion I wish to acknowledge my indebtedness to the University of Sydney, and especially to the Anatomy Department of its Medical School, for the conveniences and valuable material placed at my disposal; also to Professors A. N. Burkitt and C. W. Stump and Dr H. J. Wilkinson for the loan of private books, for help in obtaining references, and for their suggestions and readiness to confirm or criticise any dissection that seemed unusual; and to the technical staff to whom I am indebted for the preparation of microscopic slides, photo-micrographs, and other things indispensable to the carrying out of this dissection.

LIST OF DRAWINGS AND THEIR LEGENDS

DIOPTOGRAMS

I. Norma Facialis.

A 1. Orang. Notice the large trachelo-platysma with its aberrant sheets of muscle over the left shoulder, the apparent presence of a M. triangularis, a well-marked auriculo-labial sheet, a large M. orbito-temporalis, the meeting of the Mm. frontalis and occipitalis at vertex of head, and the large fan-shaped caput angulare lying on the same plane as the M. orbicularis oculi. Inset shows the superficial layer of the M. depressor capitis turned downwards to expose the middle layer; the dotted line indicates the line of attachment of the deep layer to the pericranium. Lateral to this is seen the attachment to the supra-orbital ridge of some fibres of the M. frontalis.

B 1. Orang. Notice that the caput angulare lies deep to the M. orbicularis oculi, and that the M. orbicularis oculi and the temporo- and auriculo-labial sheets form a continuous muscle layer.

C 1. Orang. Notice the rudimentary auriculo- and temporo-labial fibres, the well-marked M. orbito-temporalis arising deep to the M. frontalis, the absence of a M. procerus, the participation of the caput angulare in labial traction, and that the muscle lies deep to the M. orbicularis oculi.

D 1. Baboon. Notice the large caput infra-orbitale and the absence of the caput angulare, the large M. orbito-temporalis arising deep to the M frontalis, and the insertion into the ear cartilage of fibres from this muscle and from the M. frontalis.

E 1. Macaque. Notice the large caput angulare and the absence of a caput infra-orbitale; the M. orbito-temporalis is similar to that of the baboon.

II. Norma Lateralis.

A 2. Orang. Notice the same features as in A 1; also the large size of the noto-platysma, the well-marked M. auriculo-occipitalis proprius forming an unbroken fan, and a small thin sheet of the deep layer of the noto-platysma lying upon the M. trapezius and still attached to the auricle, though not to the main platysmal sheet nor the lig. nuchae.

B 2. Orang. Notice as in B 1; also there is a true M. triangularis. The aberrant fibres shown are part of this muscle. The noto-platysma is large.

C 2. Orang. Notice as in C 1; also notice the large noto-platysma, the ending of the fibres of the Mm. orbicularis oris and incisivus superior upon the platysma, and the shaded line denoting the fixation of the platysma to the mandible by fibrous arches.

D 2. Baboon. Notice as in D 1; also the large noto-platysma, the hernial protrusion of the cheek pouch through the platysmal sheet which is covered by fibres from the M. buccinator, the interlacing of the superficial layer of fibres of the portio decussata with the M. caninus, and that the M. caninus appears on the surface between the M. zygomaticus and the temporo-labial fibres. The noto-platysma is attached by muscle fibres to the ligamentum nuchae and there is a well-developed M. cervico-auriculo-occipitalis.

E 2. Macaque. Notice as in E 1. Compare the fibres of the portio decussata and the occipital region in this Primate with those of the baboon.

III. Trachelo-platysma.

A 3. Orang. Notice the different types of aberrant fibres on right side of the chest and left shoulder region; also the complexity of the portio decussata which anteriorly covers the chin (M. triangulaire interne, Cruveilhier) and laterally simulates a M. triangularis and is inseparably interlaced with the M. caninus.

C 3. Orang. Notice crossing of fibres at the lower part of the chest, and the comparatively simple portio decussata.

D 3. Baboon. Notice the large and complex portio decussata which forms a primitive M. triangularis, and that it is not attached to the caudad portion of the cheek pouches.

E 3. Macaque. Notice the portio decussata forming a primitive M. triangularis, and the left cheek pouch hooked up to show its relationship to the platysma.

IV. M. Caninus.

C 4. Orang. The M. caninus is small and lacks the caudally directed fibres. Its fibres embrace the incisivo-orbicularis sheet (cut across) which is seen ending upon the cheek. Above are seen the Mm. incisivus (cut across), labii profundus and pars alaris proprius.

D 4. Baboon. Notice the cut edge of the superficial fibres of the portio decussata, and the window in the platysma to show the deep fibres of the portio decussata passing between two layers of the labral platysma; also the decussation of these deep fibres with the M. caninus and, on the neck of the cheek pouch, of the M. incisivus inferior with the platysma. The origins of the M. incisivus inferior and the M. mentalis are intermingled.

E 4. Macaque. Notice the interlacing of the M. caninus with the portio decussata, the origins of the M. mentalis and M. incisivus inferior, and the ending of the M. incisivus inferior on the neck of the cheek pouch.

V and VI. Occipital Region.

D 5. Baboon. Notice the attachment of the noto-platysma to the lig. nuchae; the superficial and deep layers of the noto-platysma between which is arising the M. cervico-auriculo-occipitalis; the small band of the noto-platysma which is attached to the auricle.

D 6. Same as D 5 with the M. cervico-auriculo-occipitalis removed to display the deep layer of the noto-platysma and the Mm. occipitalis and auricularis posterior. Inset shows the superficial lateral fibres of the M. occipitalis removed to display the origin of the remainder of the muscle. A few anomalous fibres are seen lying deep to the M. auricularis posterior.

VII. Norma Facialis of Skulls.

In all these the numbers correspond to those given in the table of muscles at the beginning of this article.

VIII. Norma Laterales of Skulls.

IX. Bases Modioli.

These are diagrammatic but are retained amongst the dioptograms for ease of reference, e.g. A 9 represents the basis modioli of orang Z O 1, B 9 that of orang Z O 2 and so on. F 9 is that of an Australian aboriginal for purposes of comparison. Each diagram represents the attachment to the mucous membrane of the modiolar area of the muscles indicated by the various numbers. The key to these numbers is on the table of muscles. For the sake of simplicity the area of the cheek pouches is not indicated.

PHOTOGRAPHS AND DIAGRAMS

Fig. 1[1]. Panniculus incarnosus of orang.

Fig. 2. Linear representation of the platysmae of different Primates. For explanation see text, pp. 26–27.

Fig. 3. Photomicrograph of a European female to show the M. labii profundus superior. Represented diagrammatically in fig. 5.

Fig. 4. Ditto enlarged.

[1] Not reproduced.

Fig. 5. Diagram of the upper lip of a European female to show the relationship of the M. labii profundus superior (*a*) to the maxilla, the vestibule of the mouth, the M. orbicularis oris (*b*), the nasal vestibule, and the skin of the upper lip. The superior labial tractor (*c*) is shown cut obliquely.

Fig. 6. Diagram of same to illustrate the forces which cause eversion of the upper lip[1]. Acting upon the free edge of the lip will be the contraction of the M. orbicularis oris puckering the lips and thrusting them forwards in a direction *A*; the labial tractors will drag the lip cranially in a direction *C* and the resultant of these two forces will be in the direction *B*. Acting on the upper part of the lip will be the downward thrust of the M. labii profundus superior in a direction *D* and this muscle will at the same time drag the whole lip towards its area of origin on the maxilla in the direction *F*. The resultant of these forces will be in the direction *E*. Thus there are two forces *B* and *E* acting at the opposite ends of a semi-rigid bar of muscle and forming a virtual couple. In this diagram the M. orbicularis oris is represented by a shaded bar and the M. labii profundus superior by four arched lines.

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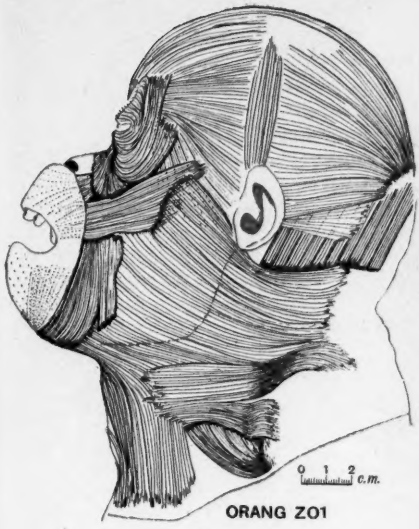
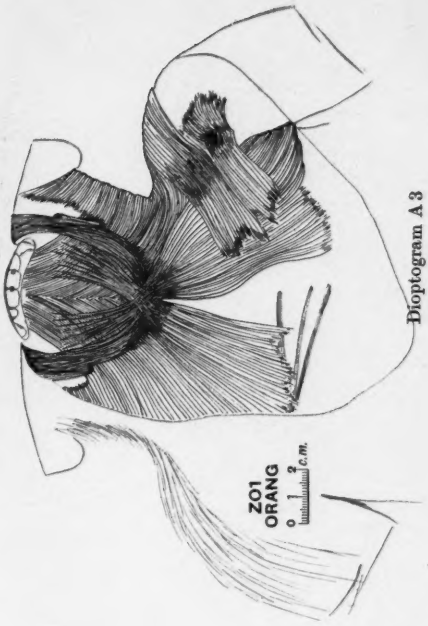
[1] During the early stages of pursing or eversion of the lips the modiolar muscles are quiescent. They come suddenly and dramatically into action when the movement is almost completed (57).

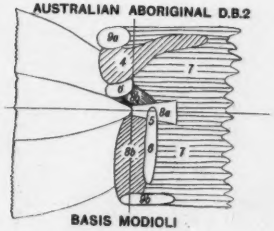


Dioptogram A 2



Dioptogram A 3

Dioptogram A 1



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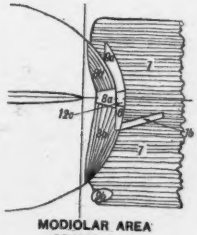

Dioptogram A 9

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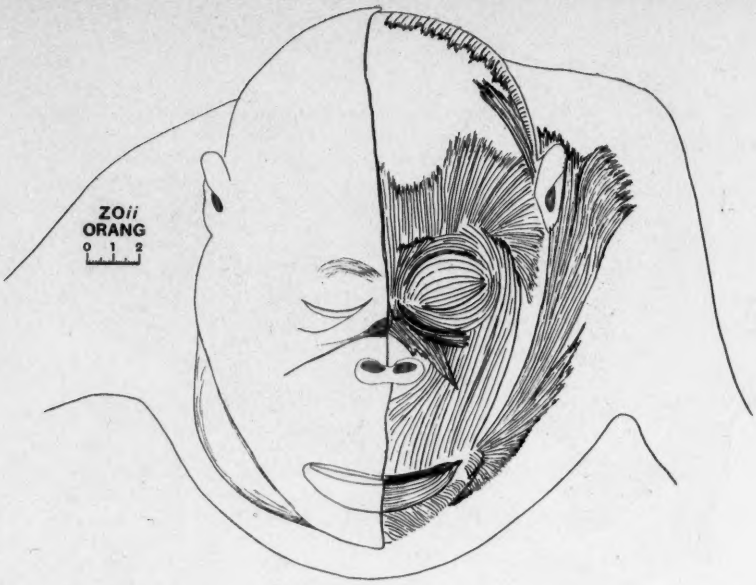
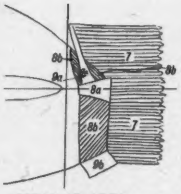


Dioptogram B 1



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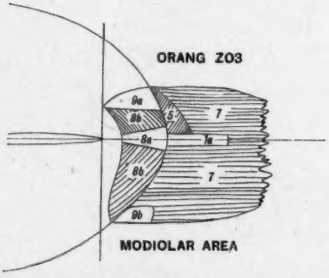

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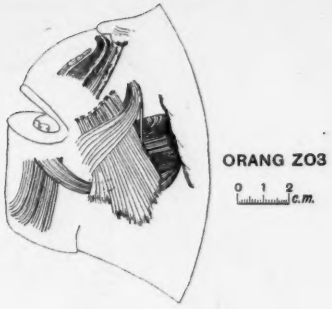

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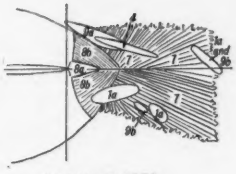

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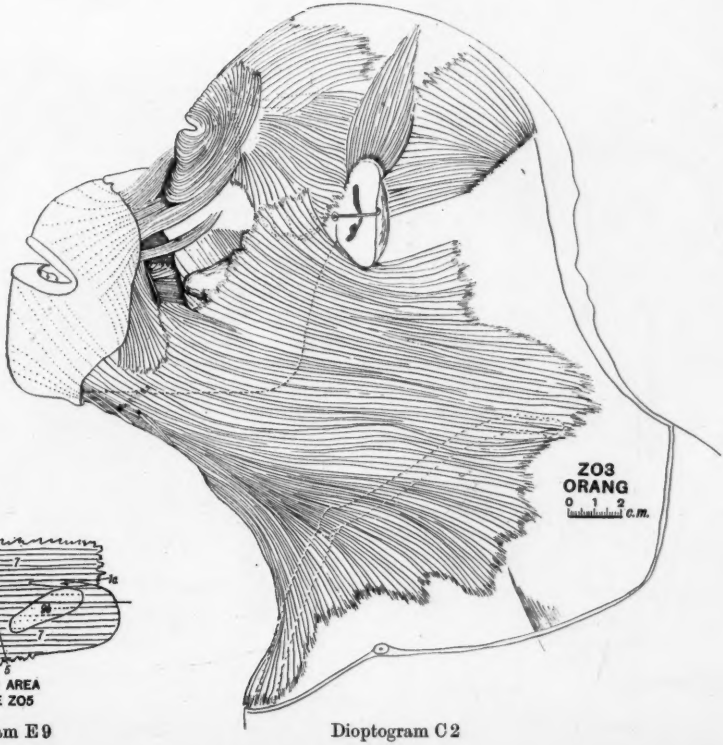

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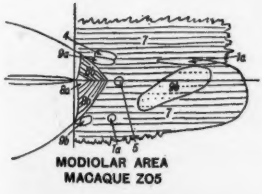

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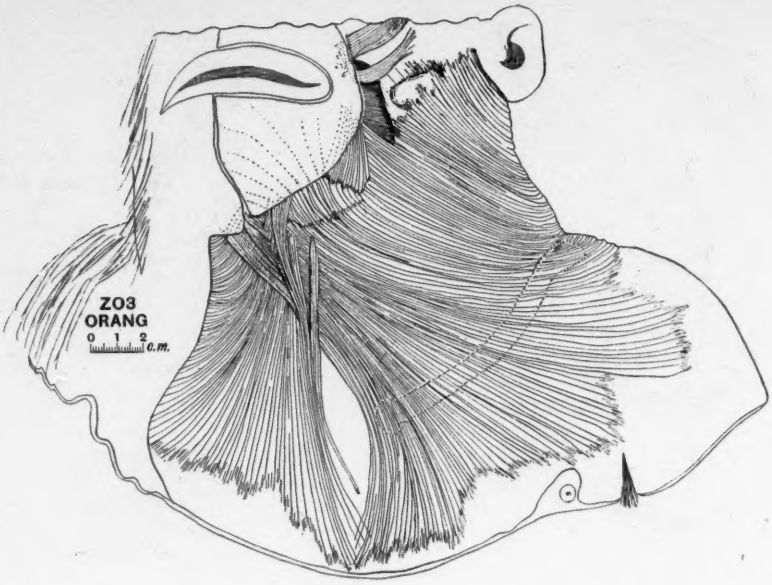

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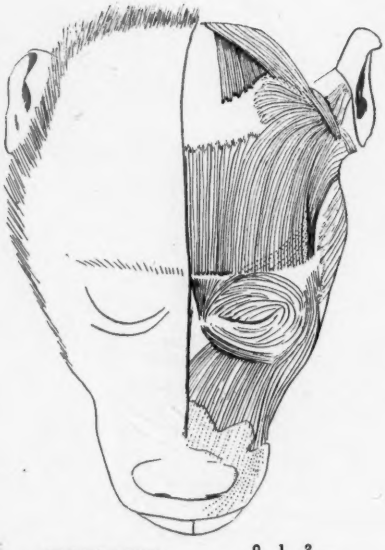

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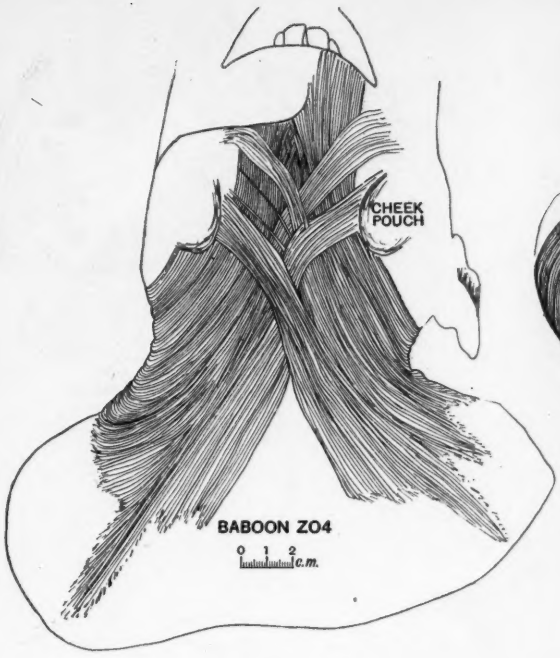

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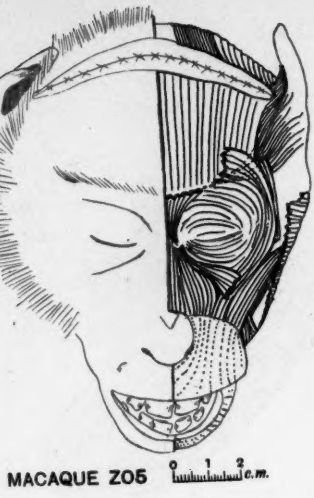

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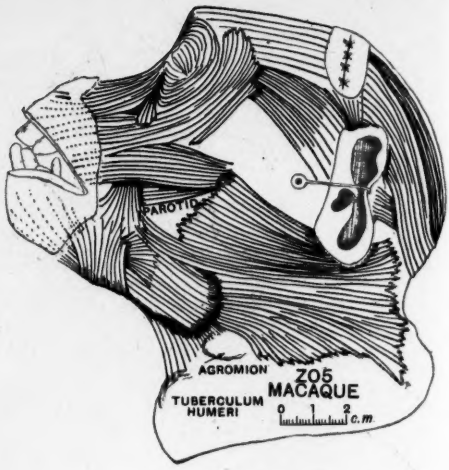

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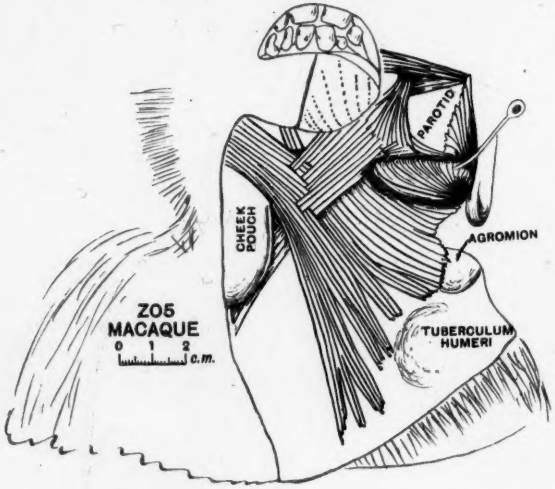

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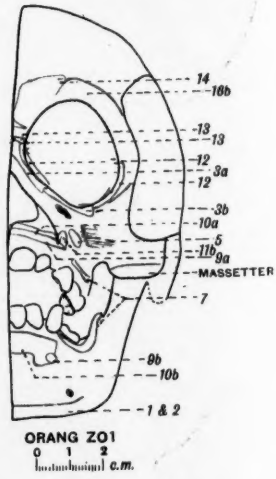
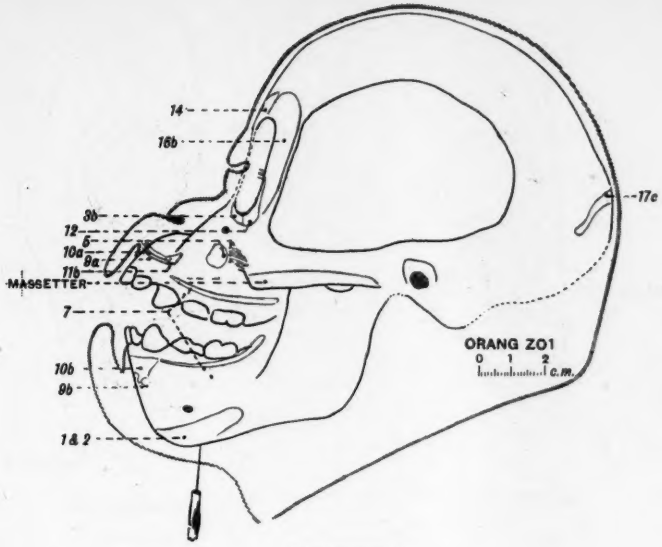
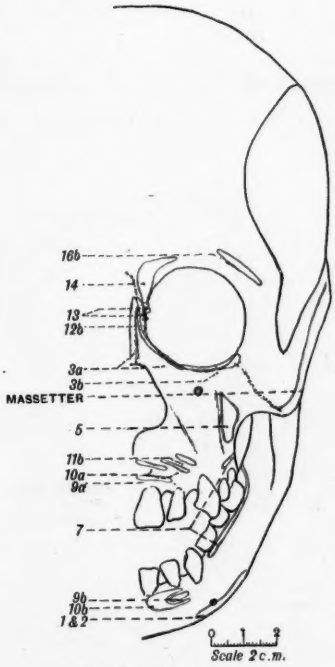


Dioptogram A 7

Dioptogram E 4



Dioptogram A 8



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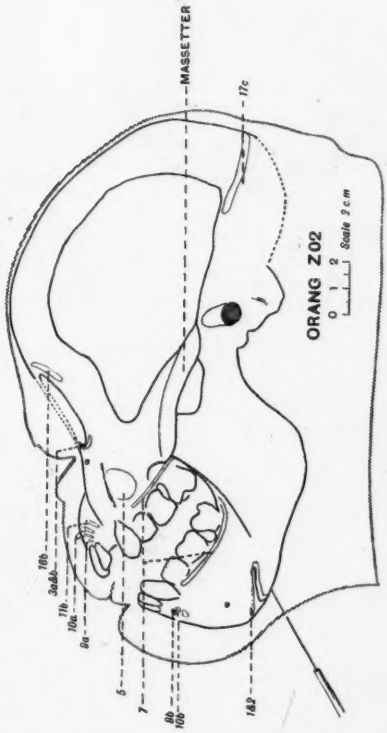

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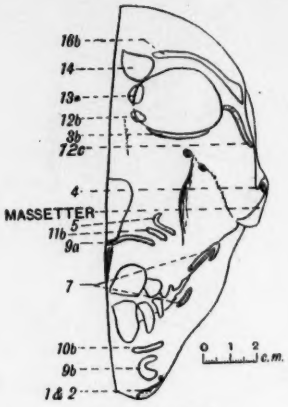
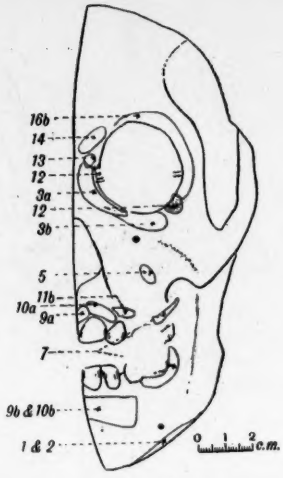


BABOON ZO4

Dioptogram D 7



ORANG ZO3

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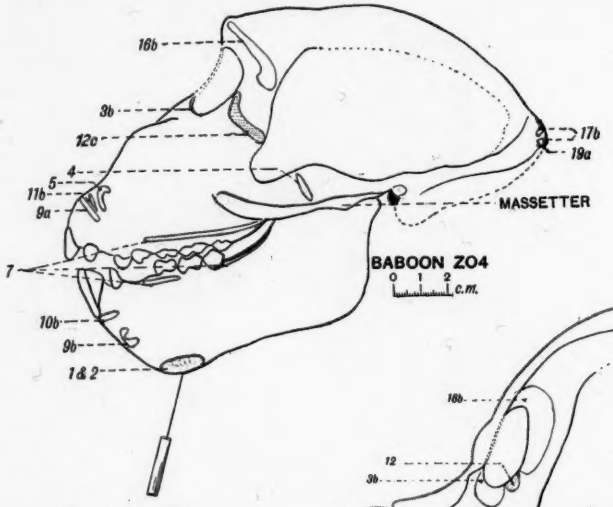

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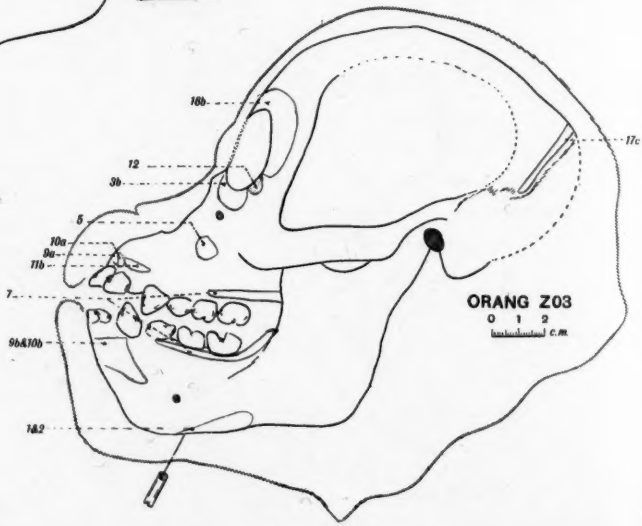

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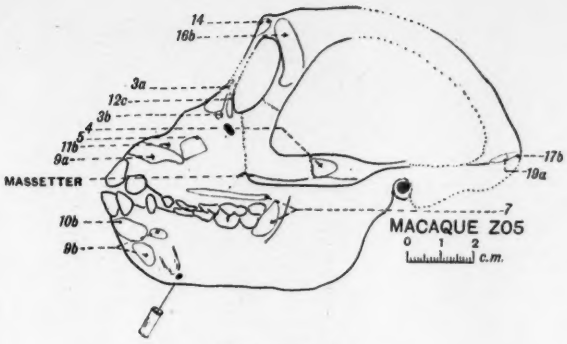

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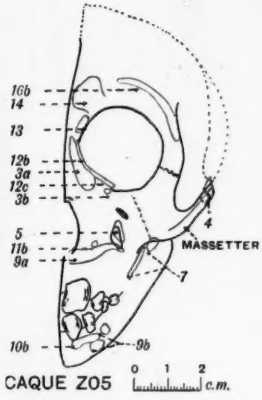

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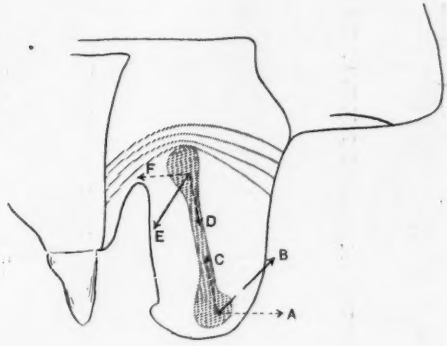
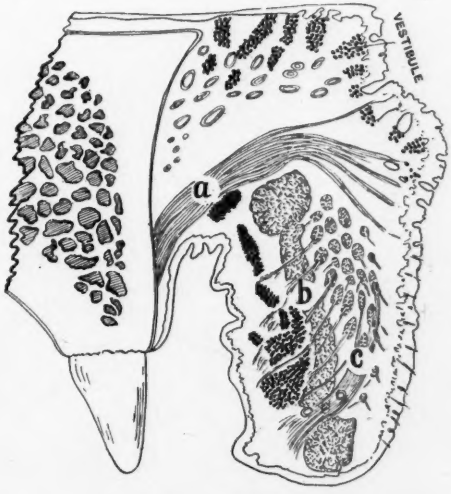


Fig. 6



HOMO SAPIENS LABIUM SUPERIUS

Fig. 5

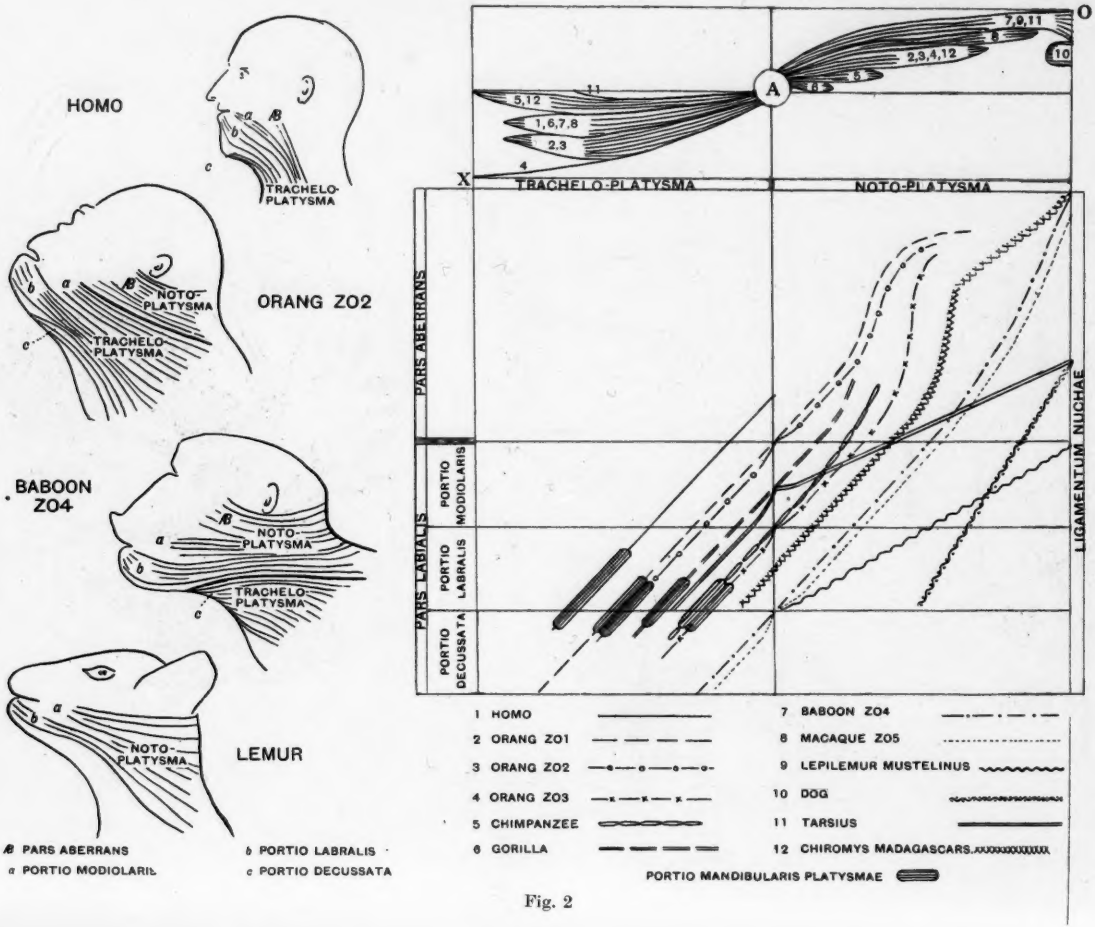

HOMO
TRACHELO-PLATYSMA
ORANG ZO2
NOTO-PLATYSMA
TRACHELO-PLATYSMA
BABOON ZO4
NOTO-PLATYSMA
TRACHELO-PLATYSMA
LEMUR
NOTO-PLATYSMA
Æ PARS ABERRANS
a PORTIO MODIOLARIS
b PORTIO LABRALIS
c PORTIO DECUSSATA
O
X
A
7,9,11
8
2,3,4,12
10
5,12
11
1,6,7,8
2,3
4
TRACHELO-PLATYSMA
NOTO-PLATYSMA
PARS ABERRANS
PARS LABIALIS
PORTIO MODIOLARIS
PORTIO LABRALIS
PORTIO DECUSSATA
LIGAMENTUM NUCHAE
1 HOMO
2 ORANG ZO1
3 ORANG ZO2
4 ORANG ZO3
5 CHIMPANZEE
6 GORILLA
7 BABOON ZO4
8 MACAQUE ZO5
9 LEPILEMUR MUSTELINUS
10 DOG
11 TARSIUS
12 CHIROMYS MADAGASCARS.
PORTIO MANDIBULARIS PLATYSMAE

Fig. 2

Fig. 3

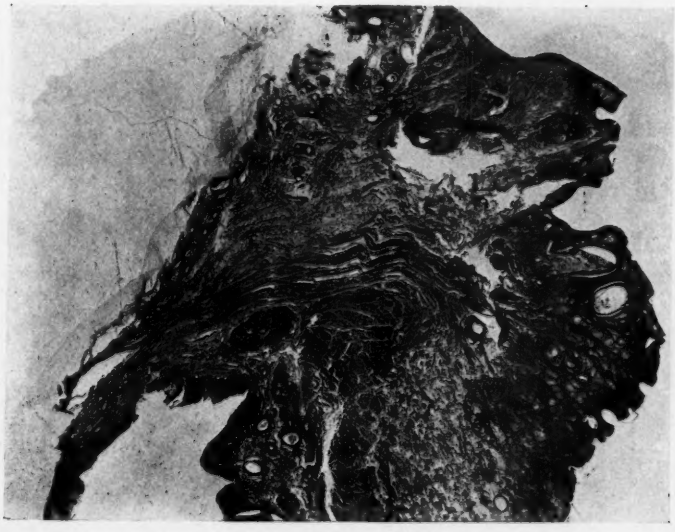


Fig. 4

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THE SURGICAL ANATOMY OF THE TONSIL[1]

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Any student of the literature of tonsillar operation must be struck by the meagre, vague and contradictory nature of the anatomical descriptions, nor can the shortcomings of the surgeons in this regard be made good by any ordinary study of the anatomists. This lack of precise anatomical teaching may to some extent account for tonsillectomy, probably the most commonly attempted of all operations, being certainly the most commonly unsuccessful.

There are obvious reasons for neglect by the two groups of investigators concerned. To the anatomist a tonsil rarely appears before an age at which it has atrophied to a shrivelled plaque, it has none of the beautiful complexity of the eye or the ear to attract study, and it belongs to that Cinderella of the systems, the Lymphatic. The surgeon on the other hand is dealing with a region difficult of access and lighting, very easily obscured by blood, and too often is using a method both blind and hurried.

I am only too conscious of the defects in the following attempt at a systematic description of those anatomical factors most important in the removal of the tonsil, an operation which is at present the only generally accepted surgical treatment of that organ. However, its conclusions have been worked out and confirmed in several thousand cases of tonsillectomy by dissection, and I hope that some of them are both useful and not usually known. At the worst the disproving of my statements may remedy the neglect which is the cause of this article.

I. DIAGRAMMATICAL REPRESENTATION OF THE TONSIL AND ITS SURROUNDINGS

The task of description of many parts of the body becomes easier if we have a simple and well-known diagram on which to work, as in the familiar cases of the tympanum, the stomach, or the colon. The diagram (fig. 1) of the tonsil and its surroundings, as seen from the inside of the pharynx, may serve this purpose.

It shows that the organ lies in a definitely triangular space, bounded by the two pillars of the fauces and the tongue. As it entirely fills this space during most of life it follows that it is itself triangular, with superior, inferior, and interior angles, and is not oval as it is usually described.

The exposed pharyngeal surface of the tonsil varies so enormously that it is hardly possible to represent it; but it is nearly always possible to distinguish the remains of the original diverticulum from which it developed. This is usually called by the obviously inaccurate name of the supra-tonsillar fossa,

[1] A paper read at the International Anatomical Congress, University College, London, April 11th, 1927.

though, as Hett pointed out, it is in the substance of the tonsil, and not above it. It is only constant in its slit-like shape, with its long axis parallel to the lingual border of the tonsillar fossa.

II. ATTACHMENTS OF THE TONSIL

Some of the organs of the body are continually exposed to forces tending to dislodge them, and to resist these forces appropriate attachments are developed. The tonsil is such an organ, and in its case one force so much outweighs any others that it need alone be considered: it is that of swallowing. Every time this occurs a powerful downward and backward impulse is given to anything lying, as the tonsil does, within the grasp of the pharyngeal constrictors.

To counteract this force there are two attachments, one fibrous and one muscular. The first is a band of fibrous tissue (figs. 5 and 6) placed just where Arbuthnot Lane's doctrine of the crystallisation of lines of force would lead one to expect it, connecting the capsule of the anterior angle of the tonsil to the base of the tongue, where it blends with the muscle sheaths. This fibrous suspensory ligament is always present, and as might be expected is most marked in large and prominent tonsils; though like all structures of the kind it is much more easily demonstrated in living tissues still fulfilling their functions, than in the blurred and matted layers of the preserved cadaver.

The second anchorage is the insertion of the decussating fibres of the palatoglossus and palatopharyngeus muscles into the lower third of the tonsillar capsule (fig. 2). This is not a mere adherence, but a definite insertion with the object of lifting the tonsil up past the descending bolus as the soft palate rises in the act of swallowing. This action may have some importance in the production of mouth breathing in children, in many of whom the tonsils are so large that an airway in the pharynx can only be obtained when the tonsils are lifted by contracting the soft palate, at the price of shutting off the nasal airway.

III. BLOOD SUPPLY OF THE TONSIL

The traditional description of the blood supply is that it comes from half a dozen arteries, and that there is on the deep surface a peritonsillar venous plexus. I believe that the tonsil is supplied like an ordinary lymphatic gland, from a single artery entering a definite hilum, from which the veins emerge. In this case the hilum is always in the lower part of the buried surface close to the tongue (fig. 2), and the artery is the tonsillar branch of the facial. The other tonsillar arteries described ramify in the muscles and mucous membrane round about, but do not pierce the capsule.

There are usually two veins, which run out from the hilum through the superior constrictor close to where the artery passes through it, to end in the common facial trunk.

In consequence of this arrangement of the blood vessels the tonsil may be separated over two-thirds of its buried surface during tonsillectomy for the loss of only a few drops of blood. When the hilum is divided the artery may

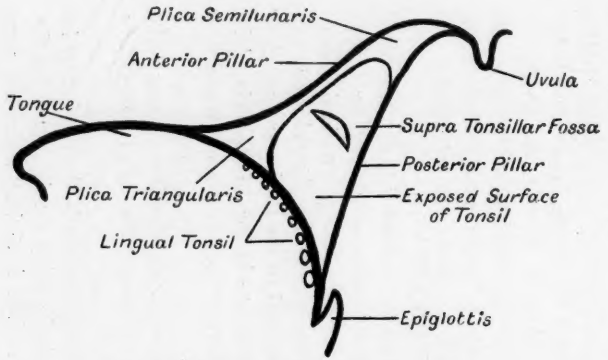

Fig. 1. Diagram of tonsil and surroundings.

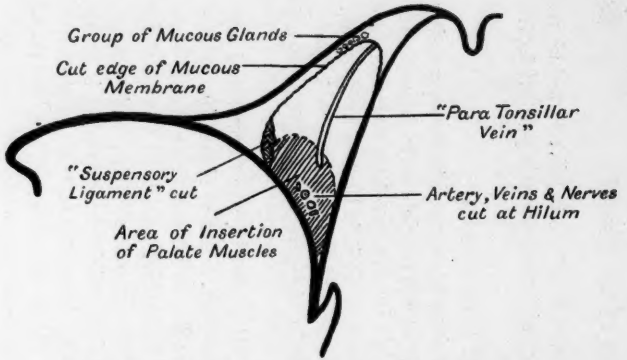
Group of Mucous Glands
Cut edge of Mucous Membrane
"Para Tonsillar Vein"
"Suspensory Ligament" cut
Artery, Veins & Nerves cut at Hilum
Area of Insertion of Palate Muscles

Fig. 2. Diagram of surroundings of tonsil after its removal.

Fig. 3. Variation in "paratonsillar vein."

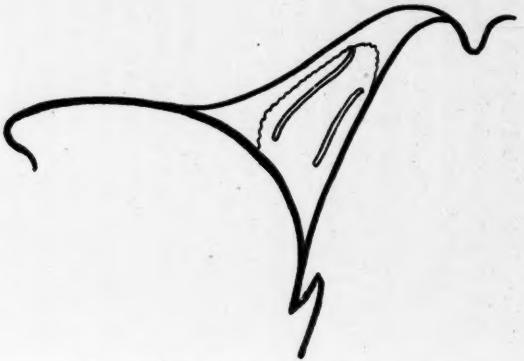

Fig. 4. Variation in "paratonsillar vein."

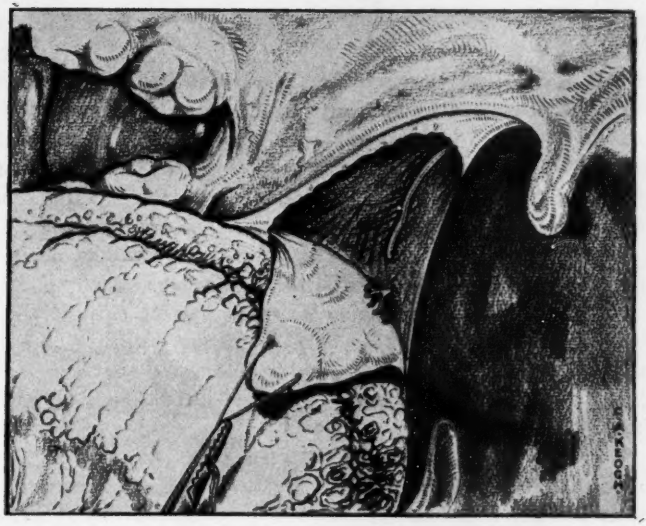

Fig. 5. Dissection of tonsil showing artery, veins and nerves entering hilum; "paratonsillar vein" lying free on the muscular bed, and suspensory ligament running from anterior angle into tongue.

Fig. 6. Drawing from an operation. Showing "paratonsillar vein" adhering to tonsil as it is dragged from its bed. The suspensory ligament is seen as it appears in tonsillectomy.

Fig. 4. Variation in "paratonsillar vein."

Fig. 3. Variation in "paratonsillar vein."

spurt freely, but then like all arteries of that size, it quickly retracts and stops bleeding. The veins are very small and never allow any considerable back flow of blood.

Where then does the bleeding, that is often so free and occasionally so dangerous, come from? I am convinced that the dangerous vessel is a vein, inconstant in its course and form as the lesser veins tend to be, which runs down from the soft palate in the areolar tissue between the capsule of the tonsil and the muscles of its bed. Below, it pierces the superior constrictor near the hilum, and enters the common facial vein. As I have said, this vein is very variable: it may take the form of several small trunks, it may run in the muscles of the tonsillar bed, or it may be absent altogether. But in its most dangerous form it is a large, single trunk running close to the capsule and often adherent to it. When the tonsil is dragged out (fig. 6) it appears to a casual glance to be running into it, and has been so described.

The peritonsillar plexus of veins, which is so often described, I believe to be entirely imaginary.

IV. NERVES OF THE TONSIL

The glossopharyngeal nerve is only separated from the lower pole of the tonsil by a thin layer of superior constrictor fibres, and the plexus which it forms with the palatine branches of the sphenopalatine ganglion gives off some surprisingly large filaments which enter the hilum. It is probably through Jacobson's nerve that the referred pain in the ear after tonsillectomy arises, though I have no notion what governs the vagaries in the occurrence and severity of it.

V. MUCOUS GLANDS NEAR THE TONSIL

There is a very constant small group of mucous glands on the anterior surface of the upper angle of the tonsil. They are adherent to the capsule on their deep surfaces, and have their ducts discharging through the mucous membrane of the anterior pillar, so that they always cause a slight difficulty in separating the tonsil at this point.

It has been suggested that their removal may cause the feeling of dryness in the throat that occasionally follows tonsillectomy, but this is difficult to believe when one considers the numbers of similar glands close by.

VI. THE SURGICAL APPLICATION OF THESE POINTS

This is obvious. The "suspensory ligament" may be divided early in the operation, thus doing away with the main anchorage of the tonsil without increasing the bleeding. It is of importance also in that when a piece of tonsil is left behind by the guillotine, its centre is almost invariably the part of the capsule fixed by this inextensible band. The "paratonsillar vein," if it should be cut, retracts into the upper angle of the tonsillar bed, where it may be caught and ligatured.

I have to thank Dr C. A. Keogh for the great care and skill with which he has drawn a very difficult subject, and Prof. Wright, of the London Hospital, for his help and encouragement in the dissections to illustrate this paper.

AN EXTREME FREE-MARTIN AND A FREE-MARTIN-LIKE CONDITION IN THE SHEEP

By J. A. FRASER ROBERTS and A. W. GREENWOOD
(*Animal Breeding Research Department, University of Edinburgh*)

Two cases exhibiting abnormalities of the reproductive system have recently been investigated by the writers and as each case presents features of rather special interest they are placed on record. The first case is that of a bovine free-martin exhibiting extreme modification in the male direction and the second is that of a lamb, a twin, the genitalia of which are similar to those found in the typical free-martin range. This second case is of interest because the occurrence of the free-martin condition in sheep has been regarded as very doubtful.

CASE I

A black Welsh calf, co-twin to a normal male, about fifteen months old when killed and examined. The animal was distinctly undersized, no doubt owing to a severe attack of parasitic bronchitis during the previous winter. In general appearance it presented a curious mixture of male and female secondary sexual characters. The head and fore-part of the body resembled those of the male, while the hindquarters more nearly resembled those of the female. It bellowed in the manner typical of the male.

The external genitalia included a vulva in the normal position. Projecting from the dorsal commissure there was a body about three-quarters of an inch across. This was dorsally curved and projected about 1 cm. On its dorsal surface the urethra opened to the exterior so that when the animal micturated the urine was projected straight up into the air. There was no trace of a scrotum or of a penis in the normal position. In the inguinal region two testis-like bodies could be palpated beneath the skin but there was no pouching of the skin.

On dissection the testes were found to lie in a pair of peritoneal evaginations situated between the muscles of the abdominal wall and the skin. In each case the cord passed through the corresponding inguinal ring.

The reproductive glands were enclosed in a typical tunica vaginalis, removal of which revealed the gonads as somewhat small (40 mm. × 25 mm.) oval bodies. These were smaller than the testes of a normal male of the same age. A well-developed epididymis divisible into head, body and tail region was present, attached to each testis, but differed from the normal in the attachment of the body of the epididymis to the gonad. In the normal male this is attached along the lateral part of the posterior border of the testis whereas in this case the attachment was along the lateral anterior border.

The rete enters from the anterior end and extends almost the whole length of the gonad. As in the cases previously described by Willier (1921) the rete was eccentrically placed and did not occupy the centre of the gonad as in the testis of the normal animal. A typical spermatic cord was present, with a well-developed vascular cord attached to the anterior end of the gonad just below the point of entrance of the rete.

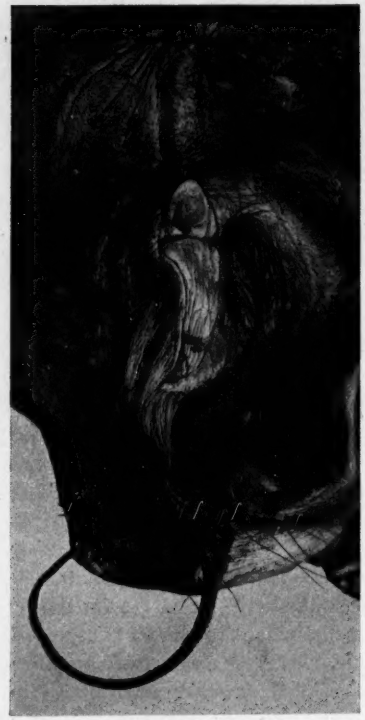

Fig. 1. Photograph of the external genitalia of free-martin calf.

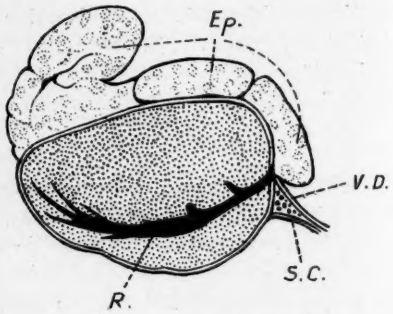

Fig. 2. Section through the gonad of free-martin calf.

Histological examination of sections from various regions of the gonads showed that the tissue consisted of somewhat small seminiferous tubules embedded in a connective tissue stroma in which abundant interstitial elements and numerous blood vessels could be identified.

Lining the thickened basement membrane of the tubules there was a single layer of epithelial cells with oval nuclei. In some cases irregular and shrunken nuclei were indicative of degeneration of some of the cells. There was no evidence of activity in these epithelial cells. The nuclei contained a comparatively large central mass consisting of several deeply stained nucleoli

embedded in a less deeply stained substance from which fine anastomosing threads radiated through the nucleus. Many large vesicles were present in the cytoplasm, particularly in the free end of the cell where, as a result, the cytoplasm was broken up into irregular strands.

The vasa deferentia were normal. There were large vesiculae seminales 4 to 5 cm. long but they were thin compared to the normal. The vasa deferentia opened into the urethra just below the seminal vesicles. The prostate was normal. There was an irregular sigmoid flexure passing into a thin penis-like body but no retractor penis muscle could be distinguished. On the dorsal aspect of the penis-like body, near the surface, was a perfect urethra. On cross-section the penis was found to be composed of a small but apparently perfect corpus cavernosum penis and a distinct corpus cavernosum urethra. The urethra opened out on the dorsal surface of the body projecting from the vulval opening as already described. There would appear to have been a rotation in development of the parts derived from the genital tubercle. Ventral to this organ the vulval opening passed into a small blind vaginal diverticulum. Apart from this there was no trace of internal female genitalia. The labia majora and minora vulvae were present. Growing from the lower commissure of the vulva was a tuft of hair about nine inches long.

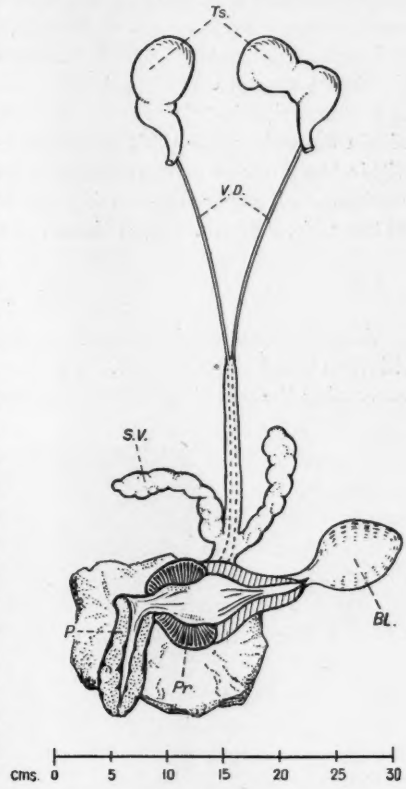

Fig. 3. Urogenital system of free-martin calf.

Case I. Discussion

The special interest of this case, an undoubted free-martin, lies in the extreme modification exhibited in the male direction. In the most extreme case of modification found by Lillie (1917) among the numerous cases examined by him (Case 44), the position of the gonads, their gross anatomy and their histology were entirely similar to the present example; but while Lillie's extreme free-martin possessed a vulva and erectile organ of the female type, in the present case this erectile organ took the form of a penis which is traversed

by the urethra. It should be specially noted that this penis did not terminate in the position normal in the male but projected a short distance beyond the dorsal commissure of the vulva. Lillie reproduces a figure illustrating an even more extreme case than any of his own. This was described by Numan (1843). This animal possessed a penis but as far as the present writers are aware, from the description given by Lillie the penis was not traversed by the urethra. It is stated that in this case of Numan's an imperforate glans penis appeared within the vulva. The position of the erectile organ was more or less central within the vulva as compared with the dorsal position in the case under discussion. As in other free-martins, the animal described in this paper showed no trace of a scrotum. These points will be considered in the general discussion.

CASE II

A Southdown-Welsh Mountain crossbred lamb, about eight to nine months old when killed and examined. It was co-twin to another lamb but information concerning the sex of the twin could not be obtained.

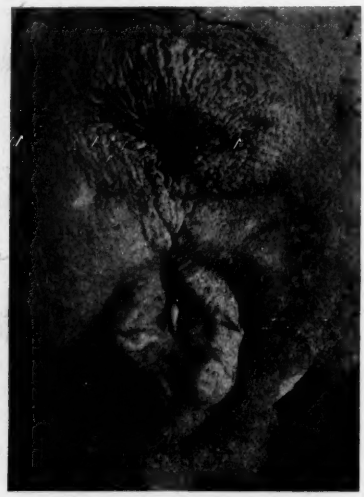

Fig. 4. Photograph of the external genitalia of abnormal lamb.

The lamb was a good, well-developed specimen of this cross. As regards secondary sexual characters it more nearly approached the male and possessed horns. Horns, however, are a variable feature in the Southdown-Welsh cross. The external genitalia were of the normal female type except that they were perhaps a little enlarged. There was no trace of scrotum or of penis. In the inguinal region two testis-like bodies could be palpated under the skin. The

external appearance of the genitalia is best summed up in the words of the owner "a ewe lamb with testicles."

On dissection the testes were found to lie in a pair of peritoneal evaginations between the muscles of the abdominal wall and the skin, in the peri-inguinal fat. In each case the cord passed through its corresponding inguinal ring.

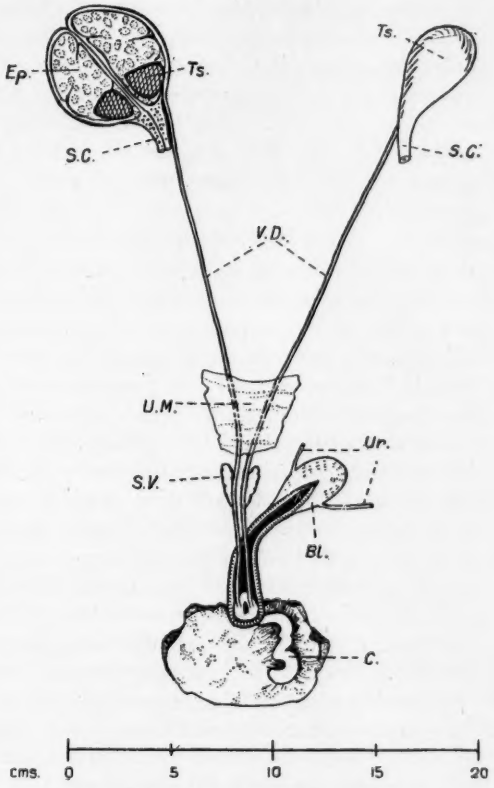

Fig. 5. Urogenital system of abnormal lamb.

The testes (15 mm. × 15 mm.) were quite small when compared with those from a normal male of the same age. There was, however, a relatively enormous development of the parts of the epididymis which showed in addition a heavy deposition of melanotic pigment in the body and tail regions. Histologically the epididymal tubules were apparently normal but were widely separated by an increase in the connective tissue elements beyond the normal.

Unfortunately, fixation of the gonads was delayed and a detailed study of the structure of the gonads was not possible. However, the gonad appeared to

consist of sex cords and small seminiferous tubules lining the thickened basement membrane of which there was a single layer of epithelial cells, embedded in a dense connective tissue stroma. The seminiferous tubules showed little evidence of convolution. Embedded in the intertubular stroma were masses of differentiated cells which appeared to resemble typical interstitial cells.

There were typical cords and typical vasa deferentia. The vesiculae seminales were of normal appearance, about two inches long. The prostate could not be recognised. The vasa deferentia opened into the uro-genital sinus on either side of the bladder opening. Ventral to the uro-genital sinus and attached about opposite to the openings of the vasa deferentia was an elongated vermiform clitoris thrown into an **S**-shaped fold, the extremity of which penetrated the mucosa in the position of a normal clitoris. Ventral to the clitoris was a very small diverticulum—there was no vagina.

Case II. Discussion

The view has been widely accepted that the free-martin condition does not occur in sheep or at least, if it does, is extremely rare. That it must be extremely rare is shown by the fact that enormous numbers of twin lambs are born annually all over the world but apparently there is no popular prejudice against females co-twin to males nor, as far as the writers are aware, has any case of a sheep free-martin been described. Lillie (1917) states that "It has been stated to occur in sheep rarely, but I cannot discover on what evidence."

The history of the present case is unfortunately not too satisfactory. The lamb was a twin but the sex of the twin is unknown. The case is placed on record because of the entire similarity between the anatomy of the lamb and of typical representatives of the bovine free-martin range. In every point of gross anatomy the case is comparable to Lillie's case 44 (1917). This condition is quite unlike the developmental intersexes, unassociated with twinning, found in the sheep and in other mammals. In this latter condition components of both male and female accessory sexual apparatus are represented and if the testes have passed through the inguinal rings a scrotum is usually found as well as at least a rudimentary penis in the normal male position. This point will be considered further in the general discussion. The writers would suggest therefore that the simplest explanation is that this lamb was a free-martin of the bovine type. The alternative view would necessitate a different mechanism producing precisely the same end result.

GENERAL DISCUSSION

These cases raise several interesting and important points in connection with the study of mammalian intersexes. Following Crew (1926–1927) mammalian intersexes can be classified into two main groups, first the developmental type assumed to be due to abnormality in the time and in the mode of differentiation of the gonads, and secondly the hormonic intersexes of the

free-martin type. The evidence for the hormonic origin on the bovine free-martin has been elaborated and perfected until to-day this theory is generally accepted. The di-zygotic origin of the twins, the vascular anastomosis, the histological findings and so on provide a mass of evidence for the hormonic theory. It would probably be true to say that the position of the developmental mammalian intersexes is not so well understood and in particular there is no general agreement as to whether they are genetic males or genetic females. It would appear to the writers that a comparison of the morphology of examples of the two groups supports the view that they are genetic males and also suggests possible criteria for a recognition of the genetic sex of mammalian intersexes.

Accepting the bovine free-martin as a genetic female a complete range of cases is found in which, with increasing modification in the male direction, the internal genitalia are largely of the male type. The derivatives of the Müllerian duct are to all intents and purposes suppressed. The external genitalia, however, present a different picture. It is significant that even in the most extreme cases no trace of a scrotum is found and although occasionally a penis-like organ is present it terminates in the vulva.

The developmental intersexes present a wide range of conditions in which the internal genitalia consist of derivatives of both Wolffian and Müllerian ducts in varying stages of development. It is however most significant that in cases where the testes have passed through the inguinal rings at least a rudimentary scrotum is present and vestiges of the penis of the male are also sometimes found. Crew (1924), describing a number of cases of developmental intersexuality in the pig, states "In a few instances there was a typical scrotum and in others the gonads could be palpated beneath the skin of the inguinal or perineal region. In all cases there was a solid conical elevation on the abdominal wall where, in the normal male, the penis ends." That even in the most extreme free-martin cases where the internal genitalia are almost completely male there should be no suggestion of the formation of scrotum or of prepuce where the penis of the male ends, points to the fact that these structures do not develop in the genetic female. There is good reason to suppose therefore that a range of individuals that include cases showing these structures are genetic males. As Crew has pointed out, the development of the external genitalia in cases in which it is assumed that this development has taken place before the influence of the differentiated gonad could be expressed leads to the production of an undifferentiated type of structure which much more nearly approximates to the female type. The influence of the differentiated male gonads would appear to be necessary for the production of the male type of external genitalia but unlike the case of the internal genitalia it is impossible for this stimulation to produce its effect except in the genetic male.

The foregoing considerations point to the conclusion that the lamb described as Case II was a free-martin.

ACKNOWLEDGEMENTS

The writers wish to express their most grateful thanks to Dr R. W. Montgomerie of the University College of North Wales, Bangor, who was instrumental in securing both animals and in addition supervised the killing and preliminary dissection. They are also greatly indebted to Mr Matthews, Veterinary Surgeon of Llanfair P.G., Anglesey, for his assistance in the dissection of the bovine free-martin; to Mr W. C. Miller of the Royal (Dick) Veterinary College, Edinburgh, for his assistance in the description of the anatomy of the genitalia; and to Dr F. A. E. Crew, Animal Breeding Research Department, for his criticism and advice.

SUMMARY

1. A bovine free-martin is described which represents extreme modification in the male direction. This animal possessed a penis, traversed by a urethra, which terminated in the vulva.

2. A sheep intersex is described, the anatomy of which is precisely similar to the bovine free-martin.

3. It is suggested that a comparison of the bovine free-martin and developmental mammalian intersexes provides evidence for the view that the latter are genetic males and further suggests criteria for the recognition of the genetic sex of such abnormal cases.

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KEY TO LETTERING

Bl. = Bladder.	*S.C.* = Spermatic cord.
C. = Clitoris.	*S.V.* = Seminal vesicles.
Ep. = Epididymis.	*Ts.* = Gonad.
P. = Penis.	*Ur.* = Ureter.
Pr. = Prostate.	*U.M.* = Urogenital fold.
R. = Rete.	*V.D.* = Vas deferens.

CONCERNING THE PITUITARY FOSSA, THE MYODOME AND THE TRIGEMINO-FACIALIS CHAMBER IN RECENT GNATHOSTOME FISHES

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Menton, France

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INTRODUCTION

Since the publication, in 1914, of my work on "The Pituitary Fossa and the Trigemino-facialis Chamber in *Ceratodus forsteri*," I have gradually formulated a theory of the origin and homologies of this part of the skull, which is a radical departure in general principle from currently accepted ideas. This theory has never been given in connected form, but nevertheless has already been called "The Allis Theory," and certain features of it have been criticised both favourably and unfavourably. If correct, it is of fundamental importance for the interpretation of this part of the vertebrate skull, and is therefore here quite fully given in so far as it relates to the chambers here under discussion. Several of the more important descriptions of this part of the skull of fishes are then reviewed in chronological order, so as to show the gradual accumulation of facts regarding it, the occasional but important errors of observation and

the various and often conflicting opinions that have been expressed regarding the origin and homologies of these chambers and their bounding walls.

The application of my theory to the interpretation of the conditions in the fishes referred to in this review is then considered.

THE ALLIS THEORY

The primitive cranium was a membranous sheath enclosing the brain, and the notochord, which lies in its floor, probably extended primarily to its anterior end. The roof of the brain developed more rapidly than its floor, and as a result of this, the brain was bent downward and forward to a greater or lesser extent over the tip of the notochord, and its membranous enclosing sheath was carried with it. The anterior surface of the primitive membranous cranium thus came to form part of the prechordal portion of the floor of the definitive cranium. The hypophysis came to lie ventral to the tip of the notochord, there being enclosed in a membranous pituitary sac formed by an evagination of the primitive cranial wall. This membranous pituitary sac was apparently a primitive feature of the vertebrate skull and forms the primary pituitary fossa.

At some period of development, the trigeminus and facialis ganglia of either side became enclosed in the lateral wall of the membranous cranium, as they actually are in the adult of the recent *Bdellostoma dombeyi* (Allis, 1903 *b*), the space in which they lay being the pars ganglionaris of the trigemino-facialis chamber and not that entire chamber, as I was formerly led to conclude. If the mesial wall of this chamber were to be broken down, the chamber would become a trigemino-facialis recess, while if this wall persisted and the lateral wall were broken down, the trigeminus and facialis ganglia would lie on the external surface of the primitive skull.

The inner layer of the membrane that forms this primitive cranium later differentiates as the dura mater, the remaining portion of the membrane either persisting as such, or undergoing chondrification or ossification. The deeper (external) layers of the dura mater are continuous with the perichondrial and periosteal membranes of the cartilages and bones so developed (Gelveden, 1925).

A so-called parachordal or basal plate was developed enclosing the notochord and apparently extended forward to, but not anterior to the anterior edge of the mandibular segment. Later, that part of the floor of the primitive cranium that lies anterior to the basal plate chondrifies in certain Vertebrates as the prootic bridge, but persists as membrane in others.

The anterior edge of this bridge, whether it be of cartilage or membrane, is directly continuous with the prechordal portion of the floor of the primitive membranous cranium.

The cartilaginous bars of the mandibular and premandibular arches had during this period and in connection with the development of a biting mouth, acquired the sigma shape and impressed it more or less completely on the more posterior arches (Allis, 1923 *b*, 1925). The dorsal ends of the pharyngeal

elements of these arches were directed toward the axial skeleton between the lateral dorsal aorta and the vein that later becomes the vena jugularis. The latter vein runs forward dorsal to the pharyngeal elements of the mandibular and premandibular arches and, anterior to the latter arch, is connected with its fellow of the opposite side either directly or by cross-commissure. This cross-commissure lies external to the primitive cranium, either ventral or posterior to the pituitary sac, and forms the future pituitary veins, one on either side.

The internal carotid artery, which forms the anterior prolongation of the lateral dorsal aorta, runs forward ventral to the pharyngeal elements of the mandibular and premandibular arches and anterior to the latter arch turns upward and perforates the primitive cranial wall to enter the cranial cavity. Slightly before it turns upward to enter that cavity, it is joined by the efferent artery of the mandibular arch. The so-called external carotid artery of fishes runs upward external to the primitive cranial wall and joining the nervus trigeminus is distributed with its several branches.

The ramus palatinus facialis of either side ran, primarily, downward between the dorsal ends of the hyal and mandibular arches and hence lay posterolateral to the pharyngomandibular.

The dorsal end of the pharyngomandibular (polar cartilage) later fuses with the parachordal plate, either with its ventral surface slightly posterior to its anterior edge, or with the latter edge. The pharyngopremandibular (trabecula), prevented from acquiring contact with the axial skeleton because of the intervening pituitary body, fuses with the distal end of the pharyngomandibular, thus giving origin to the trabeculo-polar bar.

In those fishes in which the trabeculo-polar bars fuse with the ventral surface of the parachordal plate, they later swing upward and forward so that their anterior portions come in contact with and become incorporated in the prechordal portion of the primitive cranial wall. The posterior portions of the bars do not acquire this contact, remaining below the level of the parachordal plate and enclosing between themselves and the overlying portion of the primitive cranial wall an extracranial space which primarily lay between the dorsal ends of the mandibular and premandibular arches. This space is both postpituitary and subpituitary in position, but as it has been frequently referred to in my works as the subpituitary space, it may be so designated. The pituitary veins always lie dorsal to the trabeculo-polar bars and traverse the subpituitary space. The internal carotid arteries lie primarily external to the subpituitary space ventral to the polar cartilages, but they later become enclosed between the dorsal ends of the polar cartilages, and are then pulled upward through the longitudinal space between the mesial edges of the polar cartilages of opposite sides and traverse the subpituitary space. The nervus abducens and ramus palatinus facialis of either side both run downward external to the subpituitary space across the lateral edges of the parachordal and polar cartilages.

In those fishes in which the trabeculo-polar bars fuse with the anterior end of the parachordal plate, the conditions are in principle similar to those above described, for in most of these fishes the posterior portions of these bars later become depressed below the level of the dorsal surface of the parachordal plate. In these fishes (*Teleostomi*) the internal carotid arteries do not become enclosed between the hind ends of the polar cartilages, running forward primarily ventral to these cartilages and turning upward between the hind ends of the trabeculae.

The subpituitary space is primarily without lateral bounding walls, but these walls are later formed in two distinctly different manners, giving rise to conditions that may be called Types I and II.

In Type I, the polar cartilages either fuse completely with the overlying wall of the primitive cranium, or their lateral edges fuse with that wall along the lines of the lateral edges of the prootic bridge. When they fuse completely with the cranial wall, the subpituitary space is to a large extent suppressed, but when they fuse with the primitive cranial wall by their lateral edges, they enclose the subpituitary space and give origin to the skeletal pituitary fossa, this thus being a secondary formation. In this type, the ramus palatinus facialis and the nervus abducens both lie external to the cranial wall, the pituitary vein either becoming suppressed or traversing a foramen which lies between the primitive cranial wall and the trabeculo-polar bar. In these fishes, the jugular vein and the rami palatinus and hyomandibularis facialis may become enclosed in a canal, or chamber, the lateral wall of which is formed by a posttrigeminus branchial-ray bar described immediately below, this bar not extending ventrally beyond the lateral edge of the polar cartilage and hence forming no part of the lateral wall of the pituitary fossa.

In Type II, the lateral wall of either side of the skeletal pituitary fossa is formed in part by the trabeculo-polar bar and in part by the ventral portion of the branchial-ray bar derived from the posterior row of branchial rays of the mandibular arch.

This branchial-ray bar of either side is posttrigeminus in position, lying morphologically between the nervi trigeminus and facialis. The bar fuses by its dorsal end with the dorso-lateral cupola of the otic capsule and adjacent portions of the primitive cranial wall, and its ventral end shifts its attachment from the epimandibular (palatoquadrate) to the pharyngomandibular (polar cartilage). This posttrigeminus branchial-ray bar thus encloses between itself and the cranium an extracranial space, the dorsal portion of which forms, in fishes of Type II, the pars jugularis of the trigemino-facialis chamber, while its ventral portion, which may be called the lateropituitary space, is added to the subpituitary one to form the myodomic cavity. The latter cavity is thus a tertiary formation and is not the homologue of the pituitary fossa of Type I, for in these latter fishes, the branchial-ray bar simply encloses a jugular canal or the pars jugularis of a trigemino-facialis chamber.

As the posttrigeminus branchial-ray bar shifts from the epimandibular to

the pharyngomandibular, it passes dorsal to the internal carotid artery, that artery thus thereafter lying morphologically external to it. As it fuses with the polar cartilage, it may lie partly anterior and partly posterior to the ramus palatinus facialis, that nerve thus being enclosed in a foramen which lies between the ventral end of the bar and the lateral ledge of the polar cartilage. The bar thus may have prepalatinus and postpalatinus portions, which vary in relative extent according to the point where the ramus palatinus primarily crossed the lateral edge of the polar cartilage. This nerve thus now lies in the lateropituitary space, internal to the postpalatinus portion of the branchial-ray bar. The external carotid artery may lie wholly posterior or anterior to the bar, or perforate it near its dorsal end, this depending on the position of its point of origin from the internal carotid. The jugular vein always lies internal to the bar.

The pituitary vein does not primarily traverse a definite pituitary foramen, simply passing between the primitive cranial wall and the trabeculo-polar bar to enter the subpituitary space, but in the Elasmobranchii and the Osteichthyes of my Type I it becomes secondarily enclosed in a foramen by the fusion of its bounding walls. In fishes of my Type II, where a myodomic cavity is formed by the fusion of subpituitary and lateropituitary spaces, the vein never becomes enclosed in a definite foramen, simply entering the myodome in the Teleostei through its orbital opening, and in *Amia* passing directly into the myodome from the atriopituitary space. In *Amia*, the vein always is accompanied, as it enters the myodome, by the external rectus muscle, and in the non-siluriod Teleostei by that muscle and the internal rectus.

In addition to the posttrigeminus branchial-ray bar, there may be a pretrigeminus bar which is derived from the anterior row of branchial rays of the mandibular arch. The latter bar therefore lies between the nervi trigeminus and profundus and may be either of cartilage or membrane. Its dorsal end fuses with the lateral wall of the primitive cranium in the alisphenoid region, dorsal to the vena jugularis. Its ventral end shifts inward from the epimandibular to the distal end of the pharyngomandibular (polar cartilage), either passing over the efferent mandibular artery, or enclosing that artery to a certain extent in its ventral edge. When the bar is of cartilage, it encloses between itself and the cranial wall an extracranial space which leads from the orbit into the myodome and may be called the atriopituitary space.

In *Ceratodus*, the posttrigeminus and pretrigeminus branchial-ray bars retain their primitive connection with the epimandibular (palatoquadrate) and fusing with it, become, respectively, the processus oticus and ascendens quadrati.

The so-called otic process of the Notidanidae is the homologue of the processus metapterygoideus of the Holostei and Teleostei, and hence cannot be the homologue of the otic process of *Ceratodus*, since that process is represented, as above explained, in the lateral wall of the trigemino-facialis chamber.

REVIEW

GEGENBAUR, 1872

Describes the conditions in several of the Plagiostomi.

In the Selachii, the pituitary fossa is large and long, is bounded posteriorly by the dorsum sellae and anteriorly by the preclinoid wall which is called by Gegenbaur a transverse "Wulst." In certain of these fishes, the bounding walls of this fossa are everywhere lined with the tough glistening membrane (dura mater) which forms my primitive membranous pituitary sac, and in these fishes the cartilaginous basis cranii, immediately posterior to the fossa, is more or less vacuolated. This vacuolated space is traversed by the internal carotid arteries and a canalis transversus which is considered by Gegenbeur to be a definite and independent perforation of the basis cranii, and this canal is said to give passage to a lymph vessel which connects large orbital sinuses, one on either side of the head. In others of these fishes, the vacuolated portion of the basis cranii has become incorporated in the hind end of the skeletal pituitary fossa, there being separated from the remainder of the fossa by the dura mater. This posterior portion of the fossa of these fishes and the vacuolated portion of the basis cranii in others is therefore my subpituitary space.

In the Batodei, there is neither dorsum sellae nor preclinoid wall and hence no skeletal pituitary fossa. The pituitary body is however certainly enclosed in a membranous pituitary sac, and between this sac and the basis cranii there is a subpituitary space traversed by the internal carotid arteries and Gegenbaur's canalis transversus, for I described such a space, without naming it, in *Raia* (Allis, 1912 *a*).

In certain of the Selachii, the nervi trigeminus, abducens and facialis all issue through the same foramen, but in others of them, and particularly in the Batodei, the nervi trigeminus and abducens become separated from the nervus facialis by a bar of cartilage which is now known to form part of the primitive cranial wall and is called the commissura prefacialis. In certain of these fishes this commissure becomes greatly broadened and the nervus facialis is pushed posteriorly to such an extent that its primitive simple foramen becomes a relatively long canal which opens on the outer surface of the cranium posterior to the postorbital process. This canal transmits the ramus hyomandibularis facialis, the ramus palatinus leaving it either through a perforation of its wall or by a short branch canal.

The nervus abducens and ramus palatinus facialis after issuing through the cranial wall never again perforate it, and neither of them enters at any point either the pituitary fossa, or the subpituitary space.

Gegenbaur does not describe a jugular canal as such, for he took no account of the course of the jugular vein. He however describes, in certain of these fishes, a foramen which must be the external opening of this canal, but he could find nothing issuing through it; and he also describes, in others of these

fishes, a little bridge of cartilage which would seem to form the lateral wall of a jugular canal.

The canalis transversus is said by Gegenbaur to have large funnel-shaped orbital openings, and he suggests that the myodome of the Holostei and Teleostei has been derived from this canal by certain of the recti muscles forcing their way through its orbital openings and then greatly enlarging the canal by pressure against its posterior wall; and this suggestion, by such an eminent authority, and his assumption that the canalis transversus was traversed by a lymph vessel, markedly influenced, for many years, all subsequent opinions on this subject.

Parker, 1873, 1876

Describes this region in embryos and the adult of *Salmo*, *Scyllium* and *Raia*, but gives little that is of importance in the present discussion. The myodome of *Salmo* is called the pituitary space and in the adult is roofed throughout its entire length by the prootic bridge. This bridge is perforated at about the middle of its length by a small median opening through which the pituitary body projects downward into the pituitary space, this being the pituitary opening of the brain case of my later description of *Scomber*. The ventral flanges of the prootics are said to grow downward from the investing mass.

Gegenbaur, 1878

Describes the myodome in *Alepocephalis* and says its roof is formed by the prootic bridge together with the membrane which extends from the anterior edge of that bridge to the top of the preclinoid wall. He considers this bridge and the membrane to form together part of the floor of the cranial cavity, the myodome therefore being, in his opinion, an intramural space.

Parker, 1881, 1882

Describes the so-called pituitary space in *Lepidosteus* and *Acipenser*. In a specimen of *Lepidosteus* 2 inches long, the postclinoid wall is said to be formed by a transverse bar of cartilage. In a specimen 4 inches, 5 lines long, this bar of cartilage is said to lie between the hind ends of the trabeculae, but slightly above them, and is said to cut the fenestra basicranialis into two parts, a pituitary space anteriorly and a posterior basicranial fontanelle posteriorly, the latter lying between the transverse bar of cartilage and the anterior end of the investing mass (parachordal plate). This however is evidently a misconception of the conditions, for the transverse bar of cartilage lies definitely above the basicranial fenestra and cannot cut it into two parts, his posterior basicranial fontanelle being simply a perforation of the prootic bridge.

This mistake of Parker's was not recognised by Gaupp when he described the conditions in this fish in Hertwig's *Handbuch der vergleichenden und experimentellen Entwickelungslehre der Wirbeltiere*, and it is probable that this

led him, in his descriptions of *Salmo salar* in the same *Handbuch*, to call the posterior portion of this fenestra basicranialis of that fish the fenestra basicranialis posterior, thus homologising it with the similarly named fenestra of his own description of *Lacerta*, which is a fenestration of the parachordal plate. This varying use of this term is confusing, and to facilitate the descriptions and discussion I shall hereafter refer to the fenestration of the prootic bridge as the fenestra prootica medialis and that of the parachordal plate, as the fenestra mesotica medialis. The transverse bars that form the anterior edges of the prootic bridge and the parachordal plate, whether they be of membrane or of cartilage, will be called, respectively, the commissura acrochordalis and the commissura transversa, the former term being adopted from van Wijhe's (1922) descriptions of the Selachii and the latter term from that employed to designate the anterior end of the basal plate in descriptions of human embryos (Fawcett, 1910; Kernan, 1916). The commissura transversa forms the posterior boundary of the fenestra basicranialis, the commissura acrochordalis lying in the roof of the pituitary fossa and hence definitely above the latter fenestra. A prootic bridge is formed when the commissura acrochordalis extends posteriorly so as to fuse with the commissura transversa.

Sagemehl, 1883

Describes the myodome in *Amia calva* and says that its floor forms the floor of the cranial cavity. A prootic bridge is said to roof the posterior half, approximately, of the myodome, and that part of the latter cavity that lies beneath it is said to be an intramural space. The anterior portion of the myodome, anterior to the prootic bridge, is said to form part of the cranial cavity. He describes an upper lateral chamber of the myodome, which lodges the trigemino-facialis ganglion. The ramus hyomandibularis facialis issues through a foramen in the posterior wall of this chamber, the nervus trigeminus issuing through a foramen that lies between the anterior edge of the lateral wall of the chamber and the hind edge of the pedicel of the alisphenoid. The ramus palatinus facialis runs downward into the myodome and perforates its floor, there entering and running forward in a canal that lies between the chondrocranium and the underlying parasphenoid. The internal carotid artery runs forward in the same canal till it reaches a short canal that perforates the preclinoid wall, where it turns upward and enters the cranial cavity. The jugular vein is not described and no venous or lymph vessel is said to traverse the myodome.

He describes in *Lepidosteus* a so-called cross-canal, which is said to be closed at each end, and there separated from the related orbit by only a thin plate of bone. It is said that if the rectus muscle of either side were to break through this thin plate of bone and enter the cross-canal, the myodome of *Amia* would arise. He therefore considers the conditions in this fish to definitely establish the correctness of Gegenbaur's suggestion of the origin of the myodome, the

cross-canal of *Lepidosteus* thus apparently being considered by Sagemehl to be the homologue of the canalis transversus of the Selachii.

Sagemehl, 1884, 1891

Describes the myodome in the Characinidae and Cyprinidae, but makes no mention of a chamber corresponding to the upper lateral chamber of the myodome of *Amia*. The hind ends of the trabeculo-polar bars have evidently been resorbed in most, if not all of these fishes, for the ramus palatinus facialis is said to perforate the prootic bridge and, having entered the myodome, to run forward and issue through its orbital opening without having again perforated the cranial wall.

Allis, 1897 *a*, 1897 *b*

The myodome of *Amia* and its upper lateral chamber are more fully described than they were by Sagemehl in the work above referred to. The nerves related to these two chambers and the internal carotid arteries are as described by him. The piscine external carotid artery, which is not described by Sagemehl, perforates the lateral wall of the upper lateral chamber of the myodome near its hind edge and, running forward in the chamber, issues from it with the nervus trigeminus. The jugular vein, coming from the orbit, passes through the orbital opening of the myodome, which is bounded laterally by the pedicel of the alisphenoid, and then traverses the upper lateral chamber of the myodome and issues through its posterior opening. A cross-commissural venous vessel, which connects the jugular veins of opposite sides, traverses the myodome and each half of it is later called the pituitary vein. The relations of the jugular and pituitary veins to these two chambers are here for the first time described and recognised as of morphological significance.

The radix profundi, in running outward to the orbit, traverses the orbital opening of the myodome and hence lies anteromesial to the pedicel of the alisphenoid.

No lymph vessel was found traversing the myodome, and as Gegenbaur's statement that the canalis transversus of the Selachii is traversed by such a vessel was not questioned, I concluded that the myodome of *Amia* could not have been derived from that canal. It was therefore considered to be a preexisting subpituitary space into which the external rectus muscle of either side acquired entrance by forcing its way through the pituitary foramen, that foramen becoming enlarged so as to include the foramen for the nervus abducens.

The thick glistening membrane that extends from the anterior edge of the prootic bridge to the top of the preclinoid wall is considered to represent a part of the dura mater, the myodome and its upper lateral chamber therefore being intradural spaces and the homologues, respectively, of the cavernous and intercavernous sinuses and the cavum Meckelii of man.

SEWERTZOFF, 1899

Describes the chondrocranium in embryos of *Acanthias* and *Pristiurus*, and finds the dorsal ends of the trabeculo-polar bars fusing with the ventral surface of the parachordal plate at right angles to it, slightly posterior to its anterior edge. In later stages these bars are bent upward and forward so that their anterior portions lie approximately in the plane of the parachordal plate.

ALLIS, 1901

The canalis transversus of *Mustelus* is said to be traversed by a venous vessel and not a lymph one, and this venous vessel is considered to be the homologue of the pituitary cross-commissure of *Amia*. The canalis transversus of the Selachii is therefore considered to be included in the myodome of *Amia*, but not to form the whole of it.

SWINNERTON, 1902

Describes the development of the chondrocranium of *Gasterosteus*. The trabeculae are said to fuse with the anterior ends of the so-called anterior parachordals, and these latter cartilages are said to be later tilted inward and downward and slightly depressed by the pressure of the external recti muscles which run posteriorly dorsal to and then between them, thus giving origin to the bounding walls of the myodome. The hind ends of the trabeculae are said to diverge and enclose between them the pituitary fossa, this fossa being continuous with the so-called interparachordal fossa enclosed between the diverging ends of the anterior parachordals. The hind ends of the trabeculae are later resorbed, but the anterior parachordals are apparently considered to persist, for their hind ends are said to be continuous with ridge-like processes which project ventrally from the ventral surfaces of the prootics and basi-occipital.

In a 6·6 mm. specimen, "the interparachordal fossa has been carried some distance in front of the notochord, and the parachordals themselves have united across the intervening space and across the end of the notochord in such a way that this projects below, but lies quite close against the basis cranii" (p. 514). The anterior end of the parachordal plate thus developed, forms the posterior boundary of the fenestra basicranialis, for the posterior portion of this fenestra lies between the anterior parachordals and these cartilages fuse by their hind ends with the anterior end of the parachordal plate. The anterior end of the latter plate is therefore my commissura transversa, and as the parachordal plate is not perforated posterior to this commissure, there is no fenestra mesotica medialis, the space that primarily lay between the parachordals of opposite sides having been completely closed by growth of cartilage. The space between the parachordals is always considered to be continuous with that between the anterior parachordals and the trabeculae, but this is, according to my theory, wrong, for there are here two morphologically distinctly

different fenestrae, one of which lies between the parachordals in the floor of the primitive cranium and is always closed by membrane, while the other lies between the trabeculo-polar bars, opens directly into the primarily extracranial subpituitary space and is not primarily closed by membrane. The limiting line between these two fenestrae is not readily determined, for the membranes are never described in early embryos, but it must be formed by that part of the primitive cranial wall that lies between the points where the polar cartilages fuse with it. The polar cartilages are therefore quite certainly represented in this 6·6 mm. embryo by the entire anterior parachordals.

The myodome is said to have anterior, middle and posterior portions, the anterior and middle portions corresponding to the entire myodome of *Amia* and being direct derivatives of the cranial cavity. The posterior portion lies between the basioccipital and the parasphenoid and is bounded laterally by the ridge-like processes above described, and it is said to be an extracranial space which has been secondarily added to the myodome. If the conditions were as thus described, the large orbital opening of the myodome would open directly into the cranial cavity, certain of the recti muscles would pass through this opening, traverse a certain portion of the cranial cavity and then issue from it through the hind end of the basicranial fenestra. The floor of that part of the cranial cavity thus traversed by these muscles would be formed by two bands of cartilage, one on either side, and these two bands would not only be tilted inward and downward and somewhat depressed by the muscles, but their larger ventro-mesial portions would actually be cut out of the cranial wall and become longitudinal ridge-like processes projecting ventro-mesially from the cranial wall and separated from each other in the mid-ventral line by the fenestra basicranialis; and this seems wholly improbable.

A prootic process is said to grow downward from the postorbital process (supraorbital bar, Swinnerton), to pass between the trigeminus and facialis nerves and to fuse with the anterior parachordal. The trigemino-facialis ganglion lies internal to this process, but no wall separating it from the cranial cavity is described.

Allis, 1903 *a*

The conditions in the adult *Scomber* are described, and as the manuscript of this work was sent to press in 1898, no reference is made to Swinnerton's descriptions of *Gasterosteus*. The myodome is said to have three portions, which are similar to those in *Gasterosteus*. The middle portion is roofed by the prootic bridge, the anterior portion by a membrane bone which extends from the anterior edge of the prootic bridge to the dorsal edge of the preclinoid wall, this bone being an ossification of the membrane which in *Amia calva* has the same position and extent. A median perforation of this latter bone is called the pituitary opening of the brain case, the pituitary body projecting downward through it into the myodome. The floor and side walls of the anterior portion of the myodome are formed by the parasphenoid, the related portions of the

trabeculo-polar bars having been resorbed, as they are in *Gasterosteus*. The floor and the lateral walls of the middle portion of the myodome are formed by the parasphenoid and the ventral flanges of the prootics (petrosals), this also being as in *Gasterosteus*. A horizontal membrane separates the myodome into dorsal and ventral compartments. The dorsal compartment lodges the external recti muscles and the pituitary veins, the ventral compartment lodging the internal recti muscles, which are separated from each other by a median vertical longitudinal membrane.

A horizontal canal in the prootic (petrosal) is said to be traversed its full length by the jugular vein and the piscine external carotid artery. A thin plate of bone separates this canal from the myodome and its mesial wall is perforated by foramina for the profundus, trigeminus and facialis nerves. The profundus and trigeminus nerves run forward and issue through the anterior opening of the canal, the ramus hyomandibularis facialis running posteriorly and issuing through its posterior opening. The ramus palatinus facialis enters a small canal which begins in the floor of this large horizontal canal and runs downward a certain distance in the ventral flange of the prootic (petrosal), the nerve then entering the myodome and issuing through its orbital opening without again perforating the cranial wall. The larger parts of the polar cartilages are thus certainly resorbed in this fish. Because of the relations of the large horizontal canal to the nerves and blood vessels, it is said to be the homologue of the upper lateral chamber of *Amia*, but it was later recognised that it represents only the pars jugularis of that chamber.

VAN WIJHE, 1905

Describes in early embryos of *Acanthias* a polar cartilage (Polknorpel) which lies between the trabecula and the parachordal of either side and later fuses with them.

GAUPP, 1905–1906

Describes several stages in the development of *Salmo salar*. The trabeculae, anterior parachordals and parachordals are said to arise independently of each other, but soon to fuse end to end and so form continuous bars without any indication of a dorsum sellae. In early embryos, the notochord extends forward to the level of the anterior ends of the anterior parachordals and is considered to lie definitely in that part of the fenestra basicranialis that lies between the anterior parachordals, this part of the fenestra being called by Gaupp the fenestra basicranialis posterior (interparachordal fossa, Swinnerton) and being directly continuous with the anterior portion of the fenestra which lies between the hind ends of the trabeculae and is called by Gaupp the fenestra hypophyseos (pituitary fossa, Swinnerton). The notochord cannot however, according to my theory, lie morphologically in any part of the fenestra basicranialis, for the notochord lies in the floor of the primitive membranous cranium, while the fenestra lies between the primarily extracranial trabeculo-polar bars.

In later stages, the parachordals grow to such an extent that they project forward slightly beyond the tip of the notochord and Gaupp's fenestra basicranialis posterior is apparently considered to extend posteriorly between their anterior ends. A membrane is said to extend from the mesotic tissues that lie between the parachordals forward to the top of the preclinoid wall, and in this membrane, which forms the roof of the myodome, a transverse bridge of cartilage (Querbrücke) develops, this bridge extending between the anterior ends of the parachordals and lying slightly anterior to the tip of the notochord. This bridge is apparently considered by Gaupp to cut the fenestra basicranialis posterior into two parts, one lying anterior and the other posterior to the bridge. The membrane in which this bridge develops is evidently, according to my theory, a part of the floor of the primitive membranous cranium, and the parachordals develop in it, as well as the bridge that connects their anterior ends. That part of Gaupp's fenestra basicranialis posterior that lies posterior to this commissure is therefore simply an unchondrified portion of the primitive cranial wall and can form no part of the fenestra basicranialis, the posterior boundary of that fenestra being formed by the transverse bridge. This bridge is therefore a commissura transversa and the perforation of the parachordal plate posterior to it, a fenestra mesotica medialis. This conclusion is certainly correct up to this point of the descriptions, but Gaupp later says that the transverse bridge lies in the roof of the middle portion of the myodome which is not in accord with it.

The myodome is said to be developed in a manner strictly similar to that described by Swinnerton in *Gasterosteus*, and Gaupp agrees with Swinnerton that the anterior and middle portions of the myodome are intracranial and the posterior portion extracranial in origin. As the external recti muscles extend posteriorly through the hind end of the fenestra basicranialis, they force the median portion of the parachordal plate upward and so prevent its thickening, the lateral edges of the plate projecting downward and forming the lateral walls of the related portion of the myodome. The hind end of the fenestra basicranialis must therefore lie between the middle and posterior portions of the myodome and hence cannot be represented in any part of that perforation of the parachordal plate that I have above referred to as the fenestra mesotica medialis, for this latter fenestra lies in the roof of the myodome and is not, at any stage of development, traversed by the external recti muscles. The transverse bridge of Gaupp's description, which lies between the anterior ends of the parachordals, must therefore form the posterior boundary of the fenestra basicranialis, the bridge therefore lying directly above the line that separates the middle and posterior portions of the myodome and not, as Gaupp concludes, in the roof of its middle portion. The anterior parachordals, which primarily fused with the anterior ends of the parachordals, are said to now form the floor of the middle portion of the myodome. They are therefore quite certainly polar cartilages and will be hereafter so referred to.

It is therefore certain that Gaupp's transverse bridge, when first developed,

is simply a commissura transversa, but it is said to grow later both posteriorly and anteriorly, the anterior growth being the more important and carrying the anterior edge of the bridge forward between and slightly anterior to the points where the nervi abducentes perforate the floor of the primitive cranium to enter the myodome. A prootic bridge is thus developed which is strictly similar to that of *Amia* and *Lepidosteus*, but an independent commissura acrochordalis is at no time developed. This prootic bridge is moreover not an actual outgrowth of the commissura transversa, but simply a chondrification, *in situ*, of a definite part of the floor of the primitive membranous cranium. This bridge is never, at any period of its development, perforated by a fenestra prootica medialis.

A bar of cartilage is said to be developed between the parachordal cartilage and the otic capsule, the parachordal cartilage here referred to doubtless being the anterior parachordal (polar cartilage), although this is not so stated. The bar lies between the trigeminus and facialis nerves, lateral to the jugular vein, is called the commissura basicapsularis prefacialis and is quite certainly considered to be the homologue of the similarly named commissure of his own descriptions of *Lacerta* (1900). Gaupp has however here been misled through his failure to take account of the relations of these bars to the jugular vein, for the commissure lies lateral to that vein in *Salmo*, and mesial to it in *Lacerta*, there forming part of the primitive cranial wall and cutting the incisura prootica into two parts, a foramen prooticum anteriorly and a foramen faciale posteriorly. The use of this term, commissura basicapsularis prefacialis, to designate two totally different commissures is confusing, and this is increased by Gaupp's miscalling an indenture in the anterior edge of the commissure of *Salmo* the incisura prootica.

The floor of the myodome is formed by the depressed posterior portions of the trabeculo-polar bars, these portions of the bars, like the corresponding parts of *Amia*, not being resorbed and the floor of the myodome is said to form the true floor of the cranium. The lateral walls of the middle portion of the myodome are said to be formed by the ventral portions of the prefacialis basicapsular commissures. The ramus palatinus facialis of either side is said to perforate the lateral border of the membrane that later chondrifies as the prootic bridge and, running downward in the myodome, to traverse a foramen in its bounding wall similar in position to that in *Amia*. The anterior basicapsular commissure is said to arise from the parachordal between the auditory capsule and the anterior parachordal.

Veit, 1907

Describes the myodome and the trigemino-facialis chamber in a 149 mm. specimen of *Lepidosteus osseus*.

A thin plate of cartilage is said to project anteriorly and slightly downward in the cranial cavity from the dorso-anterior edge of the parachordal plate, and its lateral edges are fused with the lateral walls of the cranial cavity. It is said

to be the homologue of the prootic bridge of *Amia*. The saccus vasculosis is said to project posteriorly beneath this plate of cartilage, and the space between this plate and the basis cranii is called the cavum sacci vasculosi and is said to be the homologue of the entire myodome of *Amia* ("Es ist das derselbe Raum, der bei *Amia* die Augenmuskeln aufnimmt," p. 177).

The basis cranii is said to be perforated on either side, slightly posterior to the optic foramen, by a canal for the internal carotid artery and posterior to it there is on either side a large foramen which is said to lie between the floor and the lateral wall of the cranium and to give passage to blood vessels coming from the cranial cavity.

In each lateral wall of the cranial cavity there is a trigemino-facialis chamber which is large above and tapers ventrally to a narrow end. This chamber lies wholly anterior to the cavum sacci vasculosi, its dorsal half lying dorsal to the plane of the parachordal plate and its ventral half ventral to that plane. The dorsal half lodges the trigemino-facialis ganglion, a foramen in its anterior wall giving passage to the nervi trigeminus and abducens and a foramen in its posterior wall to the ramus hyomandibularis facialis. The ramus palatinus facialis runs downward in the ventral half of the chamber and issues through a foramen at its ventral end and then runs forward between the chondrocranium and the parasphenoid and enters the orbit. The chamber is closed toward the cranial cavity by the dura mater, that membrane extending from the dorsal edge of the chamber to the ventro-mesial edge of the palatinus foramen.

The nervus profundus runs forward in the cranial cavity and issues through an independent foramen, not entering at any point the trigemino-facialis chamber.

Allis, 1909–1910

The myodome and trigemino-facialis chamber are described in a considerable number of teleosts, and also in *Lepidosteus* and *Lacerta*, and as the manuscript of this work was sent to press in 1907, no reference is made to Veit's work above reviewed.

In most of the non-siluriod teleosts examined, the conditions are similar to, or readily deducible from those in either *Scomber* or *Salmo*. In others of these fishes, in which the conditions are markedly different to those in *Scomber* and *Salmo*, they are nevertheless apparently deducible from them, but the membranes of the region are not sufficiently described to warrant discussion. In *Cottus*, the lateral wall of the trigemino-facialis chamber is of membrane, there therefore being no chamber in the prepared skull of these fishes.

The floor and side walls of this part of the skull of these fishes are said to be double, the myodome and trigemino-facialis chambers lying between them and therefore being intramural in position. The myodome and trigemino-facialis chamber are nevertheless still said to be the homologues of the cavernous and intercavernous sinuses and the cavum Meckelii of man.

In a large specimen of *Lepidosteus osseus*, the prootic bridge projects forward and downward in a curved line and meets and fuses with the dorsal surface of the basis cranii, thus enclosing a space which is filled with highly vasculated tissue and is said to be the cross-canal of Sagemehl's description of this fish and to correspond to that part of the myodome of *Amia* that lies beneath its prootic bridge. In Sagemehl's specimen, the prootic bridge did not extend far enough ventrally to meet the basis cranii, but was connected with it by membrane. Immediately anterior to this cross-canal, there is a slight median depression in the floor of the cranial cavity which lodges the pituitary body. Anterior to this there is a slightly depressed region which extends forward to a low transverse ridge which lies between the optic foramina and forms the preclinoid wall. Between this wall and the cross-canal, the depressed region is filled with a layer of fatty tissue which is bounded dorsally by the dura mater, and the space that lies between this latter membrane and the basis cranii is said to be a subpituitary space which is the homologue of the anterior portion of the myodome of *Amia*. This however is not strictly correct, for there are here no lateropituitary spaces, as will be later explained.

Each lateral end of the preclinoid wall is traversed by a short vertical canal which opens ventrally into the canalis parabasalis and transmits the internal carotid artery. Slightly posterior to the preclinoid wall there is, on either side, a large foramen which gives passage to the pituitary vein, this vein running postero-mesially in the subpituitary space, beneath the layer of fatty tissue, and joining beneath the pituitary body its fellow of the opposite side.

In each lateral wall of the cranium there is a trigemino-facialis chamber which is said to be the homologue of that of *Amia*, but it has a bony floor lying approximately in the plane of the parachordals and its mesial wall is of bone instead of membrane. It lodges the trigemino-facialis ganglion and is traversed its full length by the vena jugularis, the nervi trigeminus and abducens and the ramus hyomandibularis facialis issuing, respectively, through foramina in its anterior and posterior walls. The ramus palatinus facialis enters a canal which begins in the bony floor of the chamber and, running ventrally in the ventral flange of the prootic, issues through the palatinus foramen and enters the canalis parabasalis, in which it runs forward into the orbit. The mesial wall of this canal for the ramus palatinus is continuous with the mesial wall of the trigemino-facialis chamber, the two together corresponding to that part of the dura mater that, in Veit's 149 mm. specimen, closes the chamber of his description toward the cranial cavity. The ventral part of his chamber has simply become contracted and opens into the floor of the dorsal portion, this explaining how this floor was formed. The ventral portion of the canal for the ramus palatinus, and the palatinus foramen, lie partly in the edge of the prootic bone and partly in the cartilage that bounds it.

The common carotid artery runs forward in the canalis parabasalis until it reaches the palatinus foramen, where it separates into its two branches. The external carotid runs upward through the palatinus foramen and, ac-

companying the ramus palatinus, enters the trigemino-facialis chamber and issues from it with the branches of the nervus trigeminus. The internal carotid runs forward in the canalis parabasalis till it reaches its own canal in the preclinoid wall, where it turns upward, traverses its canal and enters the cranial cavity.

In an 80 mm. specimen of this fish, one head of the external rectus muscle traverses the pituitary foramen with the pituitary vein and accompanies it a certain distance in the subpituitary space.

In *Amiurus*, there is immediately posterior to the pituitary body, a transverse bolster which is said to represent the cross-canal of *Lepidosteus*. McMurrich (1884) described a cavity in this bolster and considered it to be a rudiment of the myodome of *Amia* and the Teleostei, but I could find no indication of this cavity in any of my specimens. There are no pituitary veins, the pituitary region being drained by intracranial veins. It is therefore said that this fish, like *Lepidosteus*, never possessed a functional myodome.

In *Lacerta*, there is said to be a membrane which extends from the crista sellaris forward to the subiculum infundibuli and forms the roof of a space which lies between it and the basis cranii. This space is traversed by the pituitary veins and the internal carotid arteries, and is therefore a subpituitary space which is said to be the homologue of some part of the myodome of *Amia*.

Allis, 1908 *a*, 1908 *b*

These two works were written and published after the manuscript of the work just above reviewed has been sent to press. The conditions in a 75 mm. specimen of *Polypterus* and in early larval stages of *Amiurus* are described.

In *Polypterus*, the pituitary fossa is said to be traversed by pituitary veins, here for the first time described in this fish. It is further said that if the external recti muscles were to force an entrance into the pituitary fossa by traversing the foramina for these veins, it would give rise to the myodome of the Teleostei. The conditions in *Polypterus* are said to be primitive, this fish never having possessed a functional myodome. Nothing corresponding to the pedicel of the alisphenoid of *Amia* is described.

The trigemino-facialis chamber presents two portions, a trigeminus depression in the hind wall of the orbit, and a jugular canal which arises from the dorsal portion of this depression and traverses the basal portion of the postorbital process. The dorsal portion of this depression lodges the trigeminus ganglion; its ventral end is closed ventrally by the parasphenoid, and into this part of the depression a canal opens which traverses the base of the ascending process of the parasphenoid. The anterior portion of the jugular canal lies wholly in the cartilage of the chondrocranium, its posterior portion lying in a groove in that cartilage, closed laterally by the ascending process of the parasphenoid. The nervus facialis enters this canal by a foramen which lies between these two portions. The ramus hyomandibularis runs posteriorly in the canal and issues through its posterior opening, the ramus palatinus running forward and

entering the trigeminus depression where it turns downward posterior to the nervus trigeminus and then forward ventral to it and onward into the orbit. The vena jugularis, traced forward, traverses the jugular canal and enters the trigeminus depression, where it has the same course as the ramus palatinus in that depression. The common carotid artery traverses the canal in the basal portion of the ascending process of the parasphenoid and when it reaches the ventral end of the trigeminus depression, separates into its two branches. The external carotid runs upward in the trigeminus depression, accompanying the ramus palatinus, and is distributed with the branches of the nervus trigeminus. The internal carotid runs forward into the orbit and enters the cranial cavity either through the optic foramen or through an independent foramen that lies immediately posterior to it.

In early larvae of *Amiurus*, the jugular vein and the internal and external carotid arteries are said to lie everywhere external to the cranial wall, the internal carotid entering the cranial cavity through the optic foramen, as it does in *Polypterus*. There is therefore said to be no indication of a trigemino-facialis chamber in this fish. A short posterior portion of the trabecula of either side persists and is said to lie in a little pocket on the dorsal surface of the parasphenoid and to be connected posteriorly with the prootic cartilage.

Veit, 1911

Describes several early stages in the development of the cranium of *Lepidosteus*. In 8 to 10 mm. embryos, the trabecular, polar and parachordal cartilages of either side are independent of each other, but they soon fuse to form a continuous bar which lies in the plane of the parachordals. The notochord extends forward beyond the parachordal plate to the level of the anterior ends of the polar cartilages. Later the hind ends of the trabeculo-polar bars become tilted inward and downward, but there is no indication that there has been actual depression of these parts of the bars.

In 11 to 12 mm. embryos, a bar of cartilage is said to develop between the lateral edge of the parachordal and the otic capsule. In a 14 mm. specimen, this bar is said to be a lateral extension of the cranial floor, which would seem to mean that it arises from the polar cartilage and not from the parachordal. It is said to lie external to the trigemino-facialis ganglion and between the nervus trigeminus and ramus hyomandibularis facialis. The ramus palatinus facialis runs downward internal to this bar and crosses the lateral edge of the polar cartilage immediately anterior to the ventral end of the bar. This bar of cartilage thus forms the lateral wall of the trigemino-facialis chamber of his descriptions of a 149 mm. specimen. Immediately anterior to this, a band of cartilage is said to develop in the primitive cranial wall between the trigeminus and opticus foramina and to extend from the trabecula below to the alisphenoid (supraorbital) above. The hind edge of this band fuses with the anterior edge of the bar that forms the lateral wall of the trigemino-facialis chamber, the ramus palatinus thus being enclosed in a foramen which lies between this

plate anteriorly, the lateral wall of the trigemino-facialis chamber posteriorly and the lateral edge of the polar cartilage ventrally.

Greil, 1913

The conditions in embryos of *Ceradotus* are fully and carefully described, and in 1914 I carefully reviewed all that relates to the parts of the skull here under discussion, and they will be considered when reviewing that work.

Allis, 1914 *a*

The conditions are described in *Chlamydoselachus* and *Acanthias blainvilii*. In *Chlamydoselachus* the subpituitary space forms the hind end of the skeletal pituitary fossa. There is an acustico-trigemino-facialis recess in the lateral wall of the cranial cavity, closed toward that cavity by membrane which chondrifies to a greater or lesser extent in different specimens. In the hind wall of the orbit there is a trigemino-pituitary fossa which extends ventrally to the level of the subocular shelf. Two foramina open into this fossa, one transmitting the pituitary vein and the other the nervi trigeminus and abducens. The trigeminus ganglion lies in this fossa and the fossa is closed externally by a tough layer of connective tissue which encloses the jugular vein as it crosses the fossa.

In *Acanthias blainvillii*, there is a trigemino-pituitary fossa similar to that in *Chlamydoselachus*, and a jugular canal begins in it and runs posteriorly through the postorbital process. The nervus facialis traverses the cartilage of the cranial wall by a long canal which branches, one branch transmitting the ramus hyomandibularis and the other the ramus palatinus. Both of these canals lie ventral to the jugular canal. The conditions in this fish thus resemble those in *Polypterus*, excepting in that the canals for the rami palatinus and hymandibularis open ventral to the jugular canal instead of in its mesial wall. The nervus abducens enters the trigemino-pituitary fossa with the nervus trigeminus.

It is said that if the trigemino-facialis portion of the acustico-trigemino-facialis recess of these fishes were to fuse with the trigeminus portion of the trigemino-pituitary fossa, and with the canals that transmit the jugular vein, the rami hyomandibularis and palatinus facialis, and the canal for the external carotid which is found in certain of these fishes, the trigemino-facialis chamber of *Amia* and *Lepidosteus* would arise.

There are said to be three walls either actually or potentially present in this part of the skull of fishes. The mesial one of these three walls forms the mesial wall of the trigemino-facialis chamber of the Holostei, and the mesial wall of the trigemino-facialis recess of the Teleostei and Selachii. The middle wall forms the lateral wall of the trigemino-facialis recess and the mesial wall of the pars jugularis of the trigemino-facialis chamber of the Teleostei, and the lateral one forms the lateral wall of the trigemino-facialis chamber of all these fishes.

ALLIS, 1914 *b*

The conditions in *Ceratodus*, as described by Greil (1913) and Krawetz (1910), are considered. The pituitary fossa of this fish is said to be a non-functional myodome and is compared with that of the Holostei and Teleostei, but this is incorrect, for it does not contain either lateropituitary or atriopituitary spaces, as explained immediately below.

The space that lies between the pars ascendens of the quadrate of either side and the lateral wall of the neurocranium is said to be the homologue of the trigemino-facialis chamber of *Amia*, but it is now recognised that this extracranial space of *Ceratodus* contains also lateropituitary and atriopituitary spaces. The mesial wall of the trigemino-facialis chamber corresponds to the mesial wall of the chamber of *Amia* and is called by Greil the incisura sphenotica.

The processus ascendens and processus oticus quadrati of *Ceratodus* are therefore said to be the homologues, respectively, of the pedicel of the alisphenoid and the lateral wall of the trigemino-facialis chamber of *Amia*, this being based on the similarity of the relations of the nerves and blood vessels to these several cartilages.

It is suggested that there must have been primarily an independent mass of mesoderm cells lying along the lateral wall of the chondrocranium dorsal to the mandibular and premandibular arches, these cells undergoing chondrification, and the cartilages so formed fusing in certain fishes with the chondrocranium and in *Ceratodus* with the quadrate.

The so-called otic process of the Notidanidae is said to be the homologue of the metapterygoid process of the Holostei and Teleostei and the homologue also of the processus muscularis of *Rana*.

ALLIS, 1914 *c*

The antrum petrosum laterale of the Amphibia and Reptilia is said to be the homologue of the trigemino-facialis chamber of fishes. The processus ascendens of the Amphibia and the columella of the Reptilia are the homologues of the pedicel of the alisphenoid of *Amia*, and the processus oticus of the Amphibia and Reptilia the homologue of the lateral wall of the trigemino-facialis chamber.

ALLIS, 1915

The anterior and posterior heads of the teleostean hyomandibula are said to be serial homologues, respectively, of the processus ascendens and processus oticus quadrati of *Ceratodus*, and hence the serial homologues of the pedicel of the alisphenoid and the lateral wall of the trigemino-facialis chamber of *Amia*.

ALLIS, 1918

The prefacialis and postfacialis portions of the teleostean hyomandibula are said to be formed by branchial-ray bars developed, respectively, from certain of the branchial rays of the anterior and posterior rows of the hyal arch. The

lateral wall of the trigemino-facialis chamber of fishes is said to be formed by a branchial-ray bar developed from the posterior row of branchial rays of the mandibular arch, and the pedicel of the alisphenoid of *Amia* to be developed either from the branchial rays of the anterior row of the mandibular arch, or from those rays of the posterior row of the premandibular arch.

Lehn, 1918

Describes the cavum sacci vasculosi and trigemino-facialis chamber in a 76 mm. specimen of *Polypterus*, but adds nothing relating to these chambers to that given in my description in 1908.

Allis, 1919

The myodome and trigemino-facialis chamber are described in advanced larvae and small adults of several of the Teleostei, and comparison is made with the conditions in other fishes.

In all of the non-siluroid Teleostei examined, there are horizontal and vertical myodomic membranes which separate the myodome into dorsal and ventral compartments similar to those in *Scomber*, and in certain of these fishes the horizontal membrane arches upward to such an extent that it meets, in the median line, and fuses with the ventral surface of the membrane that forms the floor of the cranial cavity. The dorsal compartment of the myodome is therefore said to be an intradural space. The horizontal membrane may chondrify or ossify to a certain extent and because of this it is said to represent the floor of the myodome of *Amia*. The dorsal compartment of the myodome of the Teleostei is therefore considered to represent the entire myodome of *Amia*, the ventral compartment being formed by the fusion in the median line of the canales parabasales of opposite sides. This is however evidently incorrect, for in *Salmo*, where the hind ends of the trabeculo-polar bars have not been resorbed, there is nevertheless a ventral compartment of the myodome lying dorsal to these bars and canales parabasales lying ventral to them.

The trigemino-facialis chambers of *Amia* and *Lepidosteus* are said to be represented, in the Teleostei, by the trigemino-facialis recess together with the so-called trigemino-facialis chamber of my descriptions of *Scomber* and the mail-cheeked fishes, and these two parts of the chamber are called, respectively, the pars ganglionaris and the pars jugularis. The nervus abducens perforates the lateral edge of the prootic bridge to enter the dorsal compartment of the myodome and innervate the rectus externus muscle. The ramus palatinus facialis perforates the floor either of the pars ganglionaris or the pars jugularis of the trigemino-facialis chamber and traverses the dorsal compartment of the myodome to enter the ventral one, where it runs forward and enters the orbit without again traversing the cranial wall. As it traverses the dorsal compartment, it is separated from that compartment by a delicate membrane.

The perforation of the prootic bridge in *Amia* and *Lepidosteus* is said to be the homologue of the fenestra basicranialis posterior of Gaupp's descriptions

of *Lacerta*, and de Beer, in a recent work (1926 *a*, p. 278), comes independently to the same conclusion. Matthes (1922, p. 181) is, however, doubtful about this and thinks that further work on reptilian embryos is necessary before it can be considered to be definitely established, and my present work leads me to conclude that these two fenestrae are not homologous.

In *Amiurus*, the membranous pituitary sac is said to form the perichondrial lining of the pituitary fossa, as it does of the larger part of that fossa in the Selachii.

In the Selachii, the dorsal compartment of the teleostean myodome is said to have been reduced either to canals traversed by the pituitary veins and internal carotid arteries, or to some part of a deeper, posterior portion of the pituitary fossa of the chondrocranium.

The conditions in *Ceratodus*, as described by earlier authors, are fully considered.

KINDRED, 1919

In a 10 mm. specimen of *Amiurus*, the trabeculae are said to be fused with the anterior ends of the anterior parachordals, these latter cartilages evidently containing the polar cartilages, as they also do in *Gasterosteus* and *Salmo*. The so-formed trabeculo-polar bars form the lateral boundaries of a large fenestra basicranialis (fenestra hypophyseos, Kindred). The anterior ends of the parachordals diverge slightly and enclose between them, in the anterior end of the parachordal plate, a space traversed by the notochord and filled with a stroma of cartilage cells. This space is considered by Kindred to be comparable to the fenestra basicranialis posterior of Gaupp's descriptions of *Salmo*, but it seems quite certain that it is the homologue of the similarly named fenestra of that author's description of *Lacerta* and hence of what I have called the fenestra mesotica medialis.

The fusion of the primitive cranial wall with the underlying cartilages has apparently prevented the development of a prootic bridge, and the tissues that represent the commissura acrochordalis have fused completely with the commissura transversa and so given rise to that thickened and rounded anterior end of the parachordal plate that McMurrich calls the transverse bolster.

The fenestra basicranialis is closed ventrally throughout its entire extent by the parasphenoid, and that part of the fenestra that lies between the trabeculae is said to be filled with connective tissue which ossifies as the suprasphenoid, this bone fusing with the parasphenoid and forming a median longitudinal ridge on its dorsal surface. The dorso-lateral edge of this bone, on either side, extends laterally above the trabecula and after fusing with the lateral edge of the parasphenoid continues upward a short distance, there forming the ventral portion of the lateral wall of the cranium. The middle portion of that part of the trabecula that is thus enclosed later becomes resorbed, the anterior and posterior ends persisting as cartilage and lying free of and unattached to the enclosing bones. The polar cartilages are not thus ensheathed in bone, their mesial edges being separated from each other by a median fenestra

hypophyseos. The pituitary body lies above this fenestra, immediately anterior to the parachordal plate, and the membranous pituitary sac and adjacent portions of the primitive cranial wall have fused completely with the polar cartilages. The lateral edges of these cartilages have fused with the ventral edges of the prootic cartilages, the latter forming parts of the primitive cranial walls.

The parasphenoid lies directly upon the ventral surface of the polar cartilage of either side and suturates with the ventral edge of the prootic, when that bone develops.

The internal carotid artery runs upward, in early embryos, mesial to the trabeculo-polar bar, but passes through that bar to its external surface when a portion of the trabecula is resorbed, thereafter lying wholly external to the cranium. The external carotid is said by Kindred to enter the cranial cavity through the trigeminus foramen, but I did not so find it in any of my specimens, a venous vessel however always issuing through this foramen to join the jugular vein.

There is said to be no indication of a myodome in any of his specimens, the recti muscles all arising from the lateral surface of the suprasphenoid.

Kindred, 1921, 1924

Describes several stages in the early development of the skull of *Sygnathus fuscus*. Preceeding this, in 1919, I described the myodome in a 145 mm. specimen of *Sygnathus acus*.

In a 6 mm. specimen, Kindred says that: "the visceral arches are formed of dense mesenchymatous masses; procartilaginous tracts are present ventro-lateral to the otic vesicle, but were not observed ventral to the brain or lateral to the notochord. Since chondroblasts are not present except in these regions, it is probable that the chondroblasts which later form the basis cranii are proliferated from the visceral-arch masses of mesenchyme" (p. 426). The conditions in early embryos of this fish are thus definitely favourable to my theory of the visceral origin of the trabeculae and polar cartilages.

In an 8 mm. specimen, the brain is said to be enclosed in a membranous sheath which, according to my theory, forms the primitive membranous cranium. The trabeculae are said to fuse with the anterior ends of the anterior parachordals, these latter cartilages evidently containing the polar cartilages. The anterior portions of the so-formed trabeculo-polar bars fuse with each other to form the trabecula communis, the posterior portions of the bars diverging and enclosing between them a fenestra basicranialis.

A fenestra is said to be enclosed between the anterior ends of the parachordals, the notochord extending throughout its entire length and the fenestra being closed by two membranes, one lying dorsal and the other ventral to the notochord and each of them continuous at either edge with the perichondrium of the bounding cartilage. The anterior boundary of this fenestra is not described, but it must exist and must be formed by what I have called the

commissura transversa, this commissure here being of membrane formed by the fusion of the two membranes that close the fenestra just above described. This latter fenestra is considered by Kindred to be the homologue of the fenestra basicranialis posterior of Gaupp's descriptions of *Salmo*, but this is certainly wrong, for the fenestra in Salmo lies between the polar cartilages in the floor of the myodome and is not closed by membrane, while the fenestra in *Sygnathus* lies in the parachordal plate. This fenestra must therefore be the homologue of what I have called the fenestra mesotica medialis in *Salmo* and *Amiurus* and hence the homologue of the fenestra basicranialis posterior of Gaupp's descriptions of *Lacerta*. From this commissure a membrane must extend anteriorly to the preclinoid wall and form the membrane that in my 145 mm. specimen was said to form the roof of the myodome throughout its entire length.

The recti muscles are said to be inserted, in the 8 mm. specimen, on the dorsal surface of the parasphenoid at the anterior end of the fenestra basicranialis, and they are said to reach their points of insertion by passing between the trabeculae and the primitive membranous cranial wall; this again being decidedly in favour of my theory of the extracranial origin of the trabeculae and polar cartilages. The space occupied by these muscles is considered to represent the entire myodome, but there is a space posterior to it, between the trabeculo-polar bars and the primitive cranial wall, which is said to be filled with fibrous connective tissue and must represent that part of the myodome of *Amia* that lies beneath the prootic bridge.

In a 12 mm. specimen, the hypophysis is said to press the meningeal membranes downward upon the trabeculo-polar bars, immediately posterior to the recti muscles, the meningeal membranes being said to here fuse with the perichondria of the trabeculo-polar bars; but in a 45 mm. specimen the external recti have extended posteriorly and are said to force the hypophysis and the overlying brain entirely out of the myodome, this being the condition found in my 145 mm. specimen.

In 8 to 12 mm. specimens, a prootic process is said by Kindred to arise from the alisphenoid cartilage (postorbital process, Kindred), to extend downward between the trigeminus and facialis nerves and to fuse with the lateral edge of the polar cartilage (trabecula, Kindred), the perichondrial membranes of the two cartilages persisting and marking their line of fusion. This process is the evident homologue of the prootic process of Swinnerton's descriptions of *Gasterosteus*, and like that process forms the lateral wall of the trigeminofacialis chamber, this chamber probably being the pars jugularis of an entire chamber, but this cannot be definitely determined, for the mesial wall of the chamber is not described. A notch in the anterior edge of the prootic process is called the incisura prootica, Kindred having evidently been misled by Gaupp giving this name to an indenture in the anterior edge of his commissura basicapsularis prefacialis, which is the homologue of the prootic process of Kindred's and Swinnerton's descriptions.

PEHRSON, 1922

Describes several early stages in the development of the skull of *Amia*.

In the earlier stages described, a polar cartilage is recognised, but it has already fused with the trabecula and parachordal, the three cartilages all lying in the plane of the parachordal. The notochord in these early stages extends to the level of the anterior ends of the polar cartilages, but it is later resorbed or withdrawn, and extends only to the anterior end of the parachordal plate. A prootic process is said to arise from the ventral surface of the anterior cupola of the otic capsule and, extending downward between the trigeminus and facialis nerves, to fuse with a short process which projects laterally from the lateral edge of the polar cartilage. This latter process is called the prefacial basicranial commissure, and it and the prootic process are still separated from each other in an 8 mm. specimen by procartilaginous tissue. These two processes together form the lateral wall of the trigeminofacialis chamber, its mesial wall being formed by the dura mater. The ventral edge of the prootic process lies, at this stage, in the level of the parachordal plate, but later, when the myodome develops, it lies in the level of the floor of that chamber, the ventral portion of the process therefore forming the lateral wall of this part of the myodome. The internal carotid artery of either side runs upward across the anterior end of the polar cartilage, mesial to the trabecula, but it later becomes wholly enclosed in the hind end of the latter cartilage.

A cartilaginous prootic bridge has not yet developed in a 56 mm. specimen and the myodome is said to be but slightly indicated.

VAN WIJHE, 1922

Describes several stages in the early development of the chondrocranium of *Acanthias vulgaris*.

In a 23 mm. specimen, the commissure which in early embryos connects the premandibular head cavities of opposite sides has become obliterated, and is replaced by a solid strand of mesenchymatous tissue which surrounds the hook-like anterior end of the notochord and fills the space within the hook. This tissue is said to represent a part of the cartilago acrochordalis of Sonies' descriptions of the chick and duck, and as it does not chondrify in *Acanthias* it is called the acrochordalis bolster. It later shifts somewhat posteriorly along the notochord, the end of the notochord projecting anteriorly beyond it and the bolster being continued posteriorly as a thin plate of tissue which lies ventral to the notochord and is connected by connective tissue with the tissue surrounding the anterior ends of the parachordals. This bolster therefore represents my commissura acrochordalis, the space between it and the parachordals is the fenestra prootica medialis and the anterior ends of the parachordals together with the tissue connecting them, my commissura transversa.

The acrochordalis bolster is extended dorso-laterally on either side as a wing-like process which projects forward above the eyeball, and in this tissue independent antotica and supraorbitalis cartilages develop and fuse with each other to form the pleurosphenoid (alisphenoid, Sewertzoff). The ventral end of the antotica is primarily connected with the acrochordalis bolster by procartilaginous tissue, but, while still retaining this procartilaginous connection with the bolster, it shifts posteriorly and fuses with the anterior end of the parachordal of its side. The cartilago antotica is said to form the anterior boundary of an incisura antotica, the ventral boundary of which is formed by the parachordal and the posterior one by the anterior end of the otic capsule, the incisura transmitting the nervi profundus, trigeminus, abducens and facialis. The cartilago and incisura antotica of this fish are therefore the homologues, respectively, of the pila and incisura prootica of Gaupp's descriptions of *Lacerta*.

The anterior end of the parachordal of either side projects anteriorly slightly beyond the otic capsule and posterior to this, at about the middle of the length of the otic region, a plate-like process, the lamina basiotica, projects laterally and ultimately forms the floor of the otic capsule. The hyomandibula articulates with this lamina, the nervus glossopharyngeus issues from the cranium posterior to it, and the anterior edge of the lamina later extends forward nearly to the point where the nervus facialis issues from the cranium. This lamina thus represents, or at least contains, the anterior basicapsular commissure of Gaupp's descriptions of *Lacerta*. These two laminae, one on either side of the head, are said to be the homologues of what Pehrson described in embryos of *Amia* as the diverging anterior ends of the parachordals, but it would seem as if they were simply the homologues of the anterior basicapsular commissures of that author's descriptions, these commissures projecting laterally from the lateral edges of the diverging anterior ends of the parachordals.

Allis, 1922, 1923 *a*

In these two works the conditions in this part of the skull of the adults of *Polypterus* and *Chlamydoselachus* are fully described, but nothing of importance is added to my account of these fishes in 1908 and 1914.

Sewertzoff, 1923

Says that in *Acipenser* the trabeculo-polar bars fuse with the ventral surface of the parachordal plate, exactly as they do in the Selachii.

Allis, 1923 *b*, 1925

The polar and trabecular cartilages are said to be the pharyngeal elements, respectively, of the mandibular and premandibular arches. This conclusion is based primarily on the consideration of the conditions in early embryos of *Acanthias*, as described by van Wijhe (1922), but strong corroborative evidence

of it is considered to be given by the fact that it offers an explanation of the otherwise apparently inexplicable course of the efferent mandibular artery, dorsal to the trabeculo-polar bar in the Elasmobranchii and ventral to it in all other fishes.

DE BEER, 1924

Says that I make "a strong case for the polar cartilage being a pharyngo-mandibular" (p. 333). Whether the trabecula is a pharyngopremandibular or not, he considers open to question, but this question does not really affect the problem here under discussion.

DE BEER, 1925

Describes early conditions in the development of *Acipenser*. In a five days old specimen of *Acipenser stellata*, the trabecular plate is said to be continuous with the parachordals without sharp change of level, which would seem to mean that the trabeculo-polar bars fuse with the anterior end of the parachordal plate instead of with the ventral surface of that plate, as stated by Sewertzoff. The incisura prootica is said to have anterior, posterior and ventral boundaries, but no dorsal one, the conditions thus here being as in Gaupp's 31 mm. specimen of *Lacerta*. Starting from this incisura there is said to be a groove which extends posteriorly between the otic capsule and the lateral edge of the parachordal plate, this groove lodging the jugular vein, the ramus hyomandibularis facialis and the piscine external carotid (orbital artery, de Beer).

In a ten and a half days specimen, the incisura prootica has acquired a dorsal boundary and is now called the foramen prooticum. There is no prefacialis commissure separating this foramen into two parts, the nervi trigeminus, abducens and facialis all issuing through it. The nervus abducens and the ramus palatinus after issuing through the foramen run downward external to the cranial wall. The ramus hyomandibularis runs posteriorly in the jugular groove with the jugular vein and the piscine external carotid, but an outgrowth of the basal plate, and not of the polar cartilage (p. 677) is said to bridge this groove and so convert it into a jugular canal, the bridge and the groove lying wholly posterior to the ramus palatinus.

DE BEER, 1926 *a*

Describes early stages in the development of this region in an extensive series of vertebrate embryos.

In a 40 mm. specimen of *Scymnus lichia*, the pila prootica of either side is said to rise up from the anterior end of the parachordal plate and fuse with the taenia marginalis, thus evidently being the cartilago antotica of van Wijhe's descriptions of *Acanthias*. This pila forms the anterior boundary of an incisura prootica, which is traversed by the nervi profundus, trigeminus, abducens and facialis. Somewhat later, this incisura is separated into two parts by a bar of cartilage which extends from the parachordal to the taenia marginalis, this bar

lying between the nervi profundus, trigeminus and abducens anteriorly and the nervus facialis posteriorly. This bar is called by de Beer the prefacial commissure and is the homologue of the commissura basicapsularis prefacialis of Gaupp's descriptions of *Lacerta*, but not the homologue of the similarly named commissure of that author's descriptions of *Salmo*.

In early embryos of *Squalus acanthias*, the jugular vein (head vein, de Beer) is said to run upward between the nervi trigeminus and facialis, thus evidently lying directly external to the commissura prefacialis. It is said to be enclosed in a membranous sheath which is evidently the homologue of the membranous tissue which I found enclosing that vein in *Mustelus*, *Chlamydoselachus* and *Heptanchus*. Somewhat later, the lateral edge of the polar portion of the subocular shelf is said to bend upward and be prolonged as a process which passes upward lateral to the jugular vein and its enclosing membranous sheath and, dorsal to that vein, to fuse with the otic capsule. The jugular vein is thus enclosed in a canal the lateral wall of which is certainly the homologue of the lateral commissure of de Beer's later descriptions of the Holostei and Teleostei, but it is not here so designated. This commissure arises from the lateral edge of the polar cartilage and must therefore lie directly external to the prefacialis commissure, which arises from the lateral edge of the parachordal plate, and the basal portions of these two commissures have evidently fused with each other up to the level of the floor of the jugular canal. De Beer then says (p. 277) that "at the same time, the palatine and hyomandibular branches of the facial nerve, which primitively have a common foramen of exit, come to be separated by the fact that the subocular shelf nips their foramen into two by fusing across it between them. Where the palatine nerve emerges is the original anterior portion of the facial foramen just behind the prefacial commissure. The hyomandibular branch emerges from the original posterior portion of the facial foramen, and the cartilage which separates the two nerves represents the postpalatine commissure of the Teleostomes and Amphibia." This postpalatinus process of *Squalus*, as above described, lies definitely internal to the jugular vein, while the postpalatinus process of de Beer's descriptions of the Holostei and Teleostei lies just as definitely external to that vein. It is therefore probable that the two processes are not homologous. There are in fact two postpalatinus bars of cartilage developed in this part of the skull in the Teleostei. The one lies internal to the jugular vein, extends from the lateral edge of the parachordal plate to the hind edge of the prefacialis commissure, forms part of the wall of the primitive cranium and separates the rami palatinus and hyomandibularis facialis. It is found in the Teleostei and not in the Holostei, is described by de Beer but not specially named by him and may be called the postpalatinus portion of the prefacialis commissure. The other bar extends from the lateral edge of the polar cartilage to the hind edge of de Beer's lateral commissure, is found both in the Holostei and Teleostei and forms part of the lateral wall of the trigemino-facialis chamber. In *Squalus* the ventral portion of these two bars of cartilage have quite certainly

fused with each other, their dorsal ends diverging and passing the one internal and the other external to the vena jugularis. The latter one of these two processes is not described by de Beer in embryos of *Squalus*, but is shown in his fig. 13, p. 274, giving a lateral view of this part of the skull of the adult. That part of the skull of this fish that lies immediately ventral to the jugular canal is thus formed by two parts completely fused with each other, the one belonging to the primitive cranial wall and the other to a secondary wall which corresponds to the lateral wall of the trigemino-facialis chamber of the Holostei and Teleostei. The canal for the ramus palatinus passes between the postpalatinus and prepalatinus portions of these two walls, lying immediately lateral to the lateral edges of the parachordal plate and the polar cartilage. The external opening of this palatinus canal of *Squalus* is therefore quite certainly the homologue of the palatinus foramen of *Amia* and not a part of the primary foramen faciale, as de Beer concludes.

The acrochordalis commissure of van Wijhe's description is said to lie morphologically anterior to the parachordal plate and to be separated from it by a fenestra which he calls the fenestra basicranialis and which is my fenestra prootica medialis.

In a five days old embryo of *Acipenser stellata*, the pila prootica is said to rise from the anterior end of the parachordal plate, as it does in the Selachii. A membrane which is said in his earlier work (1925) to extend transversely from one sphenolateral cartilage to the other, is here said to lie wholly anterior to the pila prootica and hence necessarily anterior to the anterior end of the parachordal plate. It is called the dorsum sellae and is said to be perforated by an opening which therefore lies anterior to the anterior end of the parachordal plate. This opening is therefore my fenestra prootica medialis and, according to my theory, is simply an unchondrified portion of the primitive cranial wall and not a definite perforation of it.

The nervus abducens and the ramus palatinus facialis, after issuing from their foramina, lie wholly external to the cranial wall. The pituitary vein perforates the lateral wall of the pituitary fossa.

In *Polypterus*, there is said to be no true pila prootica, for this pila is said to always lie between the foramina for the nervi oculomotorius and profundus and these two foramina are confluent in this fish. It is said that the basal portion of the pila may be present, separating the pituitary and trigeminus foramina, but this, as will be shown later, seems improbable. That part of the cranial wall that lies between the foramina for the nervi trigeminus and profundus is said to be a secondary formation. There is said to be a true prefacialis commissure. The lateral edge of the subocular shelf grows outward, upward and inward as a postpalatinus commissure which passes lateral to the jugular vein, thus enclosing it in a jugular canal. This canal is considered to be the homologue of the jugular canal of *Acipenser*, excepting that it is not traversed by the piscine external carotid artery (orbital artery, de Beer). The latter artery is said to run upward anterior to the ramus palatinus as it does in the Selachii.

The course of the internal carotid artery in this fish is considered to be secondary.

The prootic bridge is said to be perforated by a fenestra basicranialis (my fenestra prootica medialis), and this is said to show that the cartilago acrochordalis (dorsum sellae, de Beer) "is not to be regarded as the true front edge of the parachordals" (p. 282). In his fig. 21, showing a transverse section through this region, the pituitary vein is greatly constricted as it passes between the dorso-lateral edge of the polar cartilage and the lateral edge of the prootic bridge to enter the pituitary fossa. The vein has thus the appearance of being in process of being pinched in two, and in the adult specimen described by Waldschmidt (1887), this process has gone so far that the vein is described as a cord of connective tissue. In *Amiurus* the vein has been entirely pinched in two, and the pituitary region is drained by intracranial veins, as explained in one of my works above reviewed (Allis, 1908 *a*).

In *Lepidosteus*, the processus basipterygoideus (basitrabecularis, de Beer) is said to extend laterally from the lateral edge of the trabeculo-polar bar, the ramus palatinus facialis running downward across the lateral edge of the polar cartilage immediately posterior to the process and then forward beneath it. This process and that part of the subocular shelf that lies between it and the commissura basicapsularis anterior are said to extend then laterally and upward and ultimately form lateral and postpalatinus commissures, these two commissures forming the lateral wall of the trigemino-facialis chamber. This trigemino-facialis chamber is said to be separated from the cranial cavity by the dura mater, and a prefacialis commissure does not exist.

That part of the cranial wall that lies immediately anterior to the lateral commissure is said to be formed by the pila prootica, this pila lying between the trigeminus and pituitary foramina and forming the anterior boundary of the incisura prootica. This incisura transmits the nervi profundus, trigeminus, abducens and facialis, the nervus profundus being partly imbedded in the base of the pila prootica. This is said (p. 287) to be the last appearance of the nervus profundus in the Teleostomes, but the root of this nerve, called either the radix profundi or the radix cilliaris, is found in *Amia* and many of the Teleostei (Allis, 1897 *a*, 1903 *a*). The piscine external carotid artery (orbital artery, de Beer) is said to lie mesial and hence anterior to the ramus palatinus, as it does in *Polypterus* and the Selachii. The prootic bridge is said to extend between the extreme anterior ends of the parachordals, but in Parker's specimens of this fish 2 inches and 4 inches, 5 lines long, it lies considerably anterior to the anterior end of the parachordal plate. The anterior portion of the bridge is said by de Beer to correspond to the cartilago acrochordalis of *Squalus*, and hence is my commissura acrochordalis.

The processus basipterygoideus (basitrabecularis, de Beer) is, as above stated, said to project laterally from the lateral edge of the trabeculo-polar bar, but Veit says that it is a direct anterior prolongation of the floor (lateral wall) of the trigemino-facialis chamber and I so found it in the specimens that I examined.

In *Amia*, the ramus palatinus is said to run downward in a notch that lies between the hind end of the polar cartilage and the anterior end of the basal (parachordal) plate and the lateral and postpalatinus commissures are said to grow upward on either side of it, the one thus necessarily from the polar cartilage and the other from the parachordal. In the adult of *Amia*, the palatinus foramen lies at about the anterior third of the length of the myodome, and as that part of the lateral wall of the myodome that lies posterior to this foramen and dorsal to the polar cartilage must here represent the postpalatinus commissure, it here arises from the polar cartilage and not from the basal plate. The floor of the myodome is said to form the true floor of the cranium. The anterior portion of the myodome is said to be an intracranial space, and its posterior portion to lie between the polar cartilages and hence be intramural, but it would seem to be without a proper roof, for the prootic bridge which forms its dorsal boundary is said to be a transverse ridge projecting freely into the cranial cavity and forming no part of its floor. As in *Lepidosteus*, there is no prefacialis commissure.

The pila prootica, which is present in *Lepidosteus*, is absent in *Amia*, and this is said to be due to its ventral portion having been broken down by the external rectus muscle when it forced its way into the myodome through the pituitary foramen. The pila prootica of the vertebrate skull is later said to be a bar of cartilage which fuses ventrally with the anterior extremity of the parachordal of its side, that is, either with the lateral edge of the acrochordalis cartilage (commissura acrochordalis) which forms the anterior edge of the prootic bridge, or with the lateral edge of the anterior end of the parachordal plate (commissura transversa), which forms the posterior boundary of that bridge. The externus rectus muscle always lies wholly ventral not only to this bridge, but also to the membrane that extends from the anterior edge of the bridge to the dorsal surface of the preclinoid wall and hence could not break down the basal portion of the pila prootica which lies dorsal to the bridge.

The pedicel of the alisphenoid, my parasphenoidal leg of that bone, is called the pila lateralis and is said to be a process which grows downward from the orbital cartilage (taenia marginalis) to the lateral edge of the trabeculo-polar bar. It is said to be the analogue and not the homologue of the processus ascendens quadrati of *Ceratodus* and Amphibia.

The metapterygoid process of my descriptions of *Amia* is called the otic process, and hence homologised with the otic process of *Ceratodus* and the so-called otic process of *Heptanchus*.

In *Salmo trutta*, the floor of the myodome is said to form the true floor of the cranial cavity. The myodome has the three well-known teleostean portions, and de Beer considers the anterior one to be intracranial, the middle one intramural and the posterior one subcranial. A lateral commissure is said to grow upward from the lateral edge of the subocular shelf on both sides of the ramus palatinus facialis. The dorsal portion of this commissure is said to form the lateral wall of the trigemino-facialis chamber, its ventral portion forming

the lateral wall of the intracranial portion of the myodome, the lateral walls of the intramural portion apparently being formed by the polar cartilages. Gaupp says that in *Salmo salar* the lateral wall of this latter portion of the myodome is formed by the ventral portion of his commissura basicapsularis prefacialis, which is the homologue of de Beer's lateral commissure, and that the lateral wall of the anterior portion of the myodome is formed by the primitive cranial wall.

The trigemino-facialis chamber is said to be separated into pars ganglionaris and pars jugularis by a membrane which later ossifies without previous chondrification, and doubtless because of this, de Beer says that there is no prefacialis commissure in this fish or in any of the Teleostei. This membrane however forms the lateral wall of the trigemino-facialis recess and the mesial wall of the pars jugularis of the trigemino-facialis chamber, and it therefore seems quite certain that this membrane either represents or contains the prefacialis commissure.

There is said to be no pila prootica either in this fish or any others of the Teleostei, but it would certainly seem to be represented in that part of the primitive cranial wall that lies immediately anterior to the primary trigeminus foramen, as is best shown in Kindred's descriptions of *Sygnathus*. In a 12 mm. specimen of this fish, the anteromesial boundary of the trigeminus opening of the pars jugularis of the trigemino-facialis chamber is said to be formed by a part of the primitive membranous cranial wall, but in a 45 mm. specimen this opening is said to be "closed anteriorly by a downgrowth of the alisphenoid pedicel from the postorbital process" (Kindred, 1924, p. 436). This pedicel later becomes enclosed in the anterior edge of the prootic bone, this so-called pedicel of the alisphenoid of *Sygnathus* therefore having exactly the topographical position of a pila prootica.

The prootic bridge of embryos of *Salmo trutta* is said to be formed by a membrane which extends from the lateral commissure of one side to that of the other and forms, at either end, the floor of the pars jugularis of the trigemino-facialis chamber, but this seems to be due to a misinterpretation of the conditions, for the prootic bridge is definitely a part of the primitive cranium and hence cannot extend as far as the lateral commissures which, when first developed, lie definitely external to the primitive cranium and connected with it only at their dorsal and ventral ends. The prootic bridge therefore only extends on either side as far laterally as the prefacialis commissure and the floor of the pars jugularis of the trigemino-facialis chamber must be of secondary origin.

In *Clupea*, the posterior portions of the trabeculo-polar bars are said to have been resorbed, the conditions otherwise being similar to those in *Salmo*, this thus being as in *Gasterosteus*, *Scomber* and *Scorpaena*.

In *Gadus morruha*, there is said to be apparently neither myodome nor lateral commissure, but I (Allis, 1909–1910, p. 196) found in this fish what I considered to be a regular myodome bounded laterally, on either side, by the ventral flange of the prootic, and this ventral flange is always formed by the

ventral portion of my posttrigeminus branchial-ray bar (lateral commissure, de Beer).

A pila lateralis is said not to be present in any of the Teleostei. This pila lateralis is my parasphenoidal leg of the alisphenoid and in nearly all of the Teleostei that I have examined, it is represented by a part of the ascending process of the parasphenoid which is connected with the alisphenoid dorsal to the jugular vein by ligamentous tissue.

In *Ceratodus*, the trabeculo-polar bars apparently fuse with the anterior end of the parachordal plate, but it is not so stated. In a 13 mm. specimen, the parachordal plate extends forward nearly to the tip of the notochord. Its anterior end forms the posterior boundary of the fenestra basicranialis (fenestra hypophyseos, de Beer) and is accordingly a commissura transversa. There is no fenestra mesotica medialis shown in this specimen and de Beer says that his fenestra basicranialis does not exist at any stage of development.

There is said to be a typical pila prootica which rises up from the floor of the skull, and in his figure of a 13 mm. specimen it is shown apparently arising from the lateral edge of the anterior end of the parachordal plate. In a 17 mm. specimen, a bar of cartilage is said to extend from the base of one pila prootica to that of the other and to lie slightly anterior to the tip of the notochord, extending forward from there nearly to the hind end of the saccus vasculosis. This bar of cartilage is called by de Beer the dorsum sellae, and as it lies directly above the fenestra basicranialis and slightly anterior to the parchordal plate, it is a commissura acrochordalis. The pila prootica of either side must therefore, according to my theory, arise from the lateral edge of this commissure along the line where it fuses with the dorso-lateral edge of the polar cartilage, the pila there fusing secondarily with the polar cartilage and therefore appearing to arise from the floor of the skull. The space that lies between this commissura acrochordalis and the anterior end of the parachordal plate is evidently a fenestra prootica medialis and the homologue of the fenestra of *Polypterus* and the Holostei. It is not the homologue of the fenestra mesotica medialis of *Salmo* and *Amiurus* which lies posterior to the commissura transversa and also not the homologue of the fenestra basicranialis posterior of Gaupp's descriptions of *Lacerta*, the commissura transversa being called by Gaupp the crista sellaris or dorsum sellae.

Beneath the commissura acrochordalis, between it and the trabeculo-polar bars, there is a subpituitary space which I formerly considered to be the homologue of the myodomic cavity of *Amia* and the Teleostei, but I now recognise that it is simply a subpituitary space, without the addition of lateropituitary ones and hence not a myodomic cavity. The pituitary body lies anterior to the dorsum sellae and the pituitary foramen of either side anterior to the pila prootica. There is said to be no prefacialis commissure in a 13 mm. specimen of this fish, but it is present in *Protopterus*. The space between the otic process and the lateral wall of the cranium is said not to be a trigemino-facialis chamber, and the otic and ascending processes of the palatoquadrate are said to be the

analogues and not, as I maintain, the homologues of the lateral wall of the trigemino-facialis chamber and the pedicel of the alisphenoid of *Amia*. He says that the course of the ramus palatinus facialis and its relations to the cartilages of the region show definitely that in this fish his lateral and postpalatinus commissures do not exist. The otic process is said to be identical with the similarly named process of *Heptanchus*, and the latter process to be the homologue of the metapterygoid process of the Holostei and Teleostei.

de Beer, 1926 *b*

In a 24 mm. specimen of *Torpedo marmorata*, the trabeculo-polar bars are inclined downward and forward at a considerable angle to the parachordal plate and they have apparently fused with the anterior end of that plate instead of with its ventral surface, for no dorsum sellae is shown in the figures of this embryo, or in Gegenbaur's (1872) figures of the adult Batodei. The notochord projects forward beyond the anterior end of the parachordal plate and is strongly bent upward, and the base of this part of the notochord is in contact with the hind end of the trabeculo-polar plate, the latter plate thus lying nearly at right angles to the turned up anterior end of the notochord. Between this turned up anterior end of the notochord and the trabeculo-polar plate, there must be a subpituitary space similar to that described by me in *Raia*, and this space must be traversed, as in *Raia*, by the pituitary veins and the internal carotid arteries; and the efferent pseudobranchial artery of either side after passing dorsal to the trabeculo-polar bar must enter this space to fall into the internal carotid.

A pila prootica arises from the anterior end of the parachordal plate and, extending upward, fuses with the alisphenoid cartilage (orbital cartilage, de Beer), that cartilage extending posteriorly and fusing with the otic capsule. An incisura prootica (foramen prooticum, de Beer) is thus formed and a prefacialis commissure later cuts in into the two well-known parts, a foramen prooticum and a foramen faciale. The palatinus foramen is said to be cut out of the foramen faciale, and this of course must be by a little bar of cartilage which corresponds to that part of the postpalatinus commissure of his description of the Selachii that lies mesial to the jugular vein, and which I have called the postpalatinus portion of the prefacialis commissure.

No lateral or postpalatinus commissures are described.

Allis, 1926

The conditions in the Holocephali, as described by Schauinsland (1903), Dean (1906) and myself (Allis, 1912 *b*, 1917) are considered.

The polar cartilages of these fishes fuse with the ventral surface of the parachordal plate, as they do in the Selachii, but the trabeculae instead of fusing with the distal ends of the polar cartilages either retain or reacquire connection with the axial skeleton. When therefore these cartilages later swing forward and upward, as they do in the Selachii, the polar cartilages pass

between the hind ends of the trabeculae, the anterior portions of the latter cartilages passing upward along the lateral surface of the primitive membranous cranium and acquiring a position dorsal to the forebrain. This greatly modifies the conditions in this region. The polar cartilages still form the floor of the pituitary fossa, but the lateral walls of the fossa are formed by these cartilages together with the hind ends of the trabeculae. The pituitary vein of either side perforates the lateral wall of the fossa dorsal to the trabecula, but it is greatly reduced, the pituitary region being drained to a large extent by intracranial veins. The fact that the pituitary veins traverse the fossa proves that there was primarily a subpituitary space, but it has been largely suppressed, and this is further indicated by the fact that those portions of the internal carotid arteries that, as in the Selachii, lie in this space, have completely aborted in the adult (Allis, 1912 *b*). The nervus abducens and the ramus palatinus facialis both run downward across the lateral edge of the parachordal plate and then across the lateral edge of the trabecula, not entering the pituitary fossa at any point. The efferent mandibular artery of either side enters the pituitary fossa by a foramen that lies between the trabecula and polar cartilage, thus having to those cartilages the relations that it had when they were simply the dorsal elements of normally sigma-shaped visceral arches. The dorso-posterior corner of the pterygoquadrate is extended posteriorly as a process which fuses with a shelf-like flange on the lateral surface of the otic capsule, and the vena jugularis, ramus hyomandibularis, piscine external carotid and efferent mandibular artery all lie either actually or morphologically postero-mesial to it. The process is therefore a processus metapterygoideus and the homologue of the so-called otic process of the Notadinidae.

de Beer, 1927

Describes several stages in the development of *Salmo fario*. The trabeculae and parachordal cartilages are as in the teleosts above considered. No indications of independent polar cartilages were found, but these cartilages are certainly contained in the anterior ends of the so-called parachordals. In a specimen slightly older than a 17·5 mm. one, a bar of cartilage is said to develop between the parachordals immediately anterior to the tip of the notochord, and de Beer calls it the prootic bridge. He says it lies in the roof of the myodome and it is evidently the homologue of the "Querbrücke" of Gaupp's descriptions of *Salmo salar*, which, as already stated, I consider to be a commissura transversa.

The anterior basicapsular commissure is said to arise from the parachordal not far from its anterior end, and in the angle between this commissure and the anterior end of the parachordal a postpalatinus process arises and projecting antero-laterally fuses with the distal end of a prootic process which grows inward and forward (morphologically downward) from the otic capsule; these two processes together being said to form the lateral commissure. A bar of cartilage later grows antero-mesially from the anterior edge of this lateral

commissure and, fusing with the subocular shelf anterior to the ramus palatinus, encloses that nerve in a palatinus foramen. This bar of cartilage is said to represent probably the processus basitrabecularis (basipterygoideus), but it here arises from the lateral commissure, as it does in *Lepidosteus*, and not from the subocular shelf.

Undefined anterior portions of the parachordals of this description of *Salmo fario* are evidently the anterior parachordals of Gaupp's descriptions of *Salmo salar* and hence are, as I have shown when reviewing the latter work, the polar cartilages. The anterior basicapsular and lateral commissures are both said to arise from the so-called parachordal cartilage, their bases there being in contact with each other, but, according to my theory, the anterior basicapsular commissure should arise from the parachordal and the lateral commissure be fused with the polar cartilage. The line between the parachordal and polar cartilages should therefore lie between the bases of these two commissures, and the commissura transversa should and actually does lie between the parachordals immediately posterior to this line. Further evidence in favour of this is that when the polar cartilages are later depressed to form the floor of the middle portion of the myodome, they carry with them the lateral commissures, those commissures being correspondingly lengthened, while the anterior basicapsular commissures, which ultimately form the floors of the otic capsules, retain their connection with the primitive cranium in the lines of the lateral edges of the parachordals.

DISCUSSION AND CONCLUSIONS

According to my theory, the polar cartilages fuse by their dorsal ends with the external surface of the primitive cranium at or near the anterior end of what is currently called the parachordal plate. That part of the primitive floor of the cranium that lies anterior to this plate forms the prootic bridge and its anterior portion may chondrify as the commissura acrochordalis. Between this commissure and the commissura transversa (anterior end of the parachordal plate) the floor of the primitive cranium may remain unchondrified for a certain time, this forming a fenestration of the cartilaginous prootic bridge which I have called the fenestra prootica medialis, but this fenestra is not a definite perforation of the floor of the cranium, for it always remains closed by membrane. A strictly similar fenestra, the fenestra mesotica medialis, may perforate the parachordal plate immediately posterior to the commissura transversa. The cartilago acrochordalis, which forms the commisura acrochordalis, is said to lie in the premandibular segment (van Wijhe, 1922) and the relations of the two fenestrae above referred to, to this cartilage and the commissura transversa, strongly suggest that the latter lies in the mandibular segment; and the fact that in fishes the polar cartilages always fuse with the latter commissure is strongly in favour of this view. I formerly considered these two fenestrae to be homologous, but this is certainly wrong, for in fishes, the one always lies anterior to the commissura transversa and the other posterior to it,

the two fenestrae thus having to this commissure the relations of premandibular and postmandibular intervertebral spaces.

A fenestra prootica medialis has been described in the Crossopterygii, Holostei and Dipnoi and a fenestra mesotica medialis in the Teleostei, but, so far as I recall, the two fenestrae are not both described in any one fish.

In certain of the Selachii, a membranous commissura acrochordalis has been described and it is here assumed that it is found in all of them. The space between this commissure and the parachordal plate is the fenestra prootica medialis.

The prootic bridge which, according to my theory, forms part of the floor of the primitive cranium, cannot be a transverse ridge projecting freely into the cranial cavity, as de Beer maintains; and the fact that the anterior edge of this bridge is connected by membrane with the preclinoid wall in all of the Teleostomi is strong evidence in favour of my view.

The fenestra basicranialis is not a perforation of the primitive cranial wall, but simply an opening between the trabeculo-polar bars which leads directly into the primarily extracranial subpituitary space. The anterior end of the notochord is frequently said to lie in the posterior portion of this fenestra but this is, according to my theory, wholly impossible, for the notochord lies in the floor of the primitive cranium, definitely dorsal to the fenestra. This fenestra basicranialis is not primarily closed by membrane, but when the anterior portions of the trabeculo-polar bars fuse with the wall of the primitive cranium, the related portion of the fenestra basicranialis is closed by the intervening portion of that wall. This greatly reduces the fenestra and it may be further reduced by the growth of the ventro-mesial edges of the polar cartilages toward each other and their more or less complete fusion in the median line. During this reduction of the fenestra, it becomes separated into a fenestra hypophyseos and one or two foramina or canals for the internal carotid arteries.

Any structural element developed between the trabeculo-polar bars, either as an independent element or a process directed posteriorly from the ethmoid plate is developed in the primitive cranial wall and does not primarily form part of the trabeculae.

That the trabeculo-polar bars are of visceral or at least extracranial origin would seem to be established by Kindred's descriptions of the conditions in early embryos of *Sygnathus* and *Amiurus*. In a 6 mm. specimen of the former fish, the trabeculo-polar bars have not yet chondrified and the cellular tissues from which they will be later developed are proliferated from masses of mesenchymatous tissue lying in the dorsal ends of the visceral arches. In a 8 mm. specimen of this fish, these bars have chondrified and their anterior portions and hind ends have fused with the wall of the primitive membranous cranium. In the intervening region the bars and the primitive cranial wall are, however, so widely separated from each other that the recti muscles pass freely between them to acquire insertion on the dorsal surface of the parasphenoid, and that these bars have primarily formed part of the primitive cranial wall and have

been cut out of it by the recti muscles seems wholly improbable. In early embryos of *Amiurus*, the trabeculae fuse with the primitive membranous cranial wall. In later stages their middle portions become enclosed in bony sheaths formed ventrally by the dermal parasphenoid and dorsally by a suprasphenoid developed in the primitive membranous cranial wall. The enclosed portion of each bar lies wholly free in the enclosing sheath, and that cartilages as important as these bars could have been cut out of the primitive cranial wall by a bone developed in the remainder of that wall seems wholly improbable. Add to this the fact that there seems no other way of explaining the course of the efferent mandibular artery, dorsal to the trabeculo-polar bar in the Elasmobranchii and ventral to it in all other fishes, and my contention that these bars are of visceral origin seems fairly well established.

The fenestra basicranialis is bounded posteriorly by the commissura transversa, which may be either of membrane or cartilage. The hind end of this fenestra lies actually or morphologically ventral to this commissure and so also do those portions of the polar cartilages that bound it. This fenestra cannot therefore be continuous either with the fenestra mesotica or prootica medialis.

In early embryos of the Teleostomi, the polar cartilages fuse with the anterior end of the parachordal plate, lie in the same plane as that plate and are approximately of the same thickness. The anterior end of the parachordal plate (commissura transversa) later increases much more rapidly in thickness than either the polar cartilages or the prootic bridge, and the polar cartilages, which increase in width instead of thickness, retain their connection with the lateral and ventral edges of the anterior end of the parachordal plate and are tilted inward and downward and form the lateral bounding walls of the posterior portion of the pituitary fossa, which is therefore at this period of my Type I. In *Amia*, in connection with this thickening of the anterior end of the parachordal plate, the polar cartilages are carried bodily downward slightly below the level of the dorsal surface of the parachordal plate, the pituitary fossa thus being converted into a myodome, the lateral walls of the posterior portion of which are formed by the polar cartilages together with the ventral flanges of the prootics, these latter flanges being formed by the ventral portions of the posttrigeminus branchial-ray bars (lateral commissures).

In the non-siluroid Teleostei considered in the above review, the anterior end of the parachordal plate tends to become thickened, as it does in *Amia*, but the external recti muscles, which in earlier stages of development extend posteriorly between the parachordal plate and the parasphenoid, prevent this thickening of the plate along its median line. Its lateral edges, however, extend ventrally to the same or even a greater extent than they do in *Amia*, the polar cartilages being correspondingly depressed. As a result of this, a groove is formed along the median portion of the ventral surface of the parachordal plate, beginning at the anterior edge of the plate and extending posteriorly to the anterior end of its vertebra-like hind end, this portion of the plate

therefore appearing in median vertical longitudinal section like a posterior continuation of the prootic bridge which increases gradually and but slightly in thickness. The middle and posterior portions of the myodome are thus directly continuous with each other, the opening between them representing the primitive hind end of the fenestra basicranialis, but the polar cartilages do not apparently bound this part of the fenestra, having been depressed below it. The anterior end of the parachordal plate (commissura transversa), the "Querbrücke" of Gaupp's descriptions of *Salmo salar* and the prootic bridge of de Beer's descriptions of *Salmo fario*, lies directly above the hind end of the fenestra, forming its posterior boundary, the commissure thus lying between the middle and posterior portions of the myodome and not in the roof of its middle portion, as the commissura acrochordalis always does. The fenestra mesotica medialis lies in the roof of the posterior portion of the myodome and not, like the fenestra prootica medialis, in the roof of its middle portion.

The so-called depression of the hind ends of the trabeculo-polar bars is currently attributed to pressure of the recti muscles as they pass over the bars to enter the pituitary fossa. While this may be the cause of the final depression of the bars, it cannot be the cause of their being tilted inward and downward, for this has taken place in *Polypterus* and *Lepidosteus* to as marked an extent as in other fishes, and the recti muscles do not enter the pituitary fossa of these fishes at any stage of their ontogenetic development. Furthermore, it must be, in the Teleostei, the pressure of the internal and not of the external recti that causes the depression of the polar cartilages, for the external recti are separated from the polar cartilages by the ventral compartment of the myodome.

My posttrigeminus branchial-ray bar, which is de Beer's lateral and postpalatinus commissures combined, is said to be, in certain fishes, an upgrowth either of the polar or parachordal cartilage which fuses dorsally with the otic capsule; in certain other fishes this ventral upgrowth fuses with a process which grows downward either from the otic capsule alone, from the taenia marginalis (alisphenoid cartilage) alone, or partly from one of these cartilages and partly from the other; in still others of these fishes, either the prepalatinus or the postpalatinus portion of the bar may first develop, the remainder of the bar developing as a process which grows downward from the first developed portion of the bar and fuses ventrally either with the polar or parachordal cartilage; and in a 29 days old *Salmo trutta*, the bar is said to first appear as a rod of cartilage which is wholly independent of the polar cartilage, but connected with the otic capsule by procartilaginous tissue. This development of this bar in these several different manners is certainly unfavourable to its being of cranial origin, but markedly favourable to my view that it is developed in pre-existing extracranial tissue that lies external to the jugular vein. The bar developed in this tissue would then be, from its inception, in protective relation to the jugular vein, while if it were of cranial origin, there is no apparent motive for its development, for in the early stages of its formation it would seem to offer no protection whatever to the vein.

The incisura prootica is a perforation of the primitive cranial wall closed by two membranes, the trigemino-facialis recess lying between them. The trigemino-facialis and abducens nerves perforate both of these membranes as they issue from the cranial cavity, and as they traverse the outer membrane the nervus facialis may become separated from the other nerves by a prefacialis commissure, but no such commissure is described separating the nerves as they traverse the inner membrane.

In the Selachii and Batodei, the pituitary fossa is of my Type I. In certain of these fishes, my posttrigeminus branchial-ray bar fuses in normal manner with the dorso-lateral edge of the polar cartilage and extending upwards encloses the jugular vein in a jugular canal. In certain others of these fishes, the branchial-ray bar of either side apparently becomes disintegrated and dispersed, certain of the cells however forming a connective tissue membrane which closes the trigemino-pituitary fossa and encloses a short section of the jugular vein.

In the Holocephali, the pituitary fossa is of my Type I and there are no posttrigeminus branchial-ray bars. The conditions in these fishes are abnormal but are in full accord with my theory and there seems no other way of explaining them.

In *Acipenser*, the pituitary fossa is of my Type I. The posttrigeminus branchial-ray bar arises from the dorso-lateral edge of the polar cartilage, is wholly postpalatinus in position and forms the lateral wall of a jugular canal which lies wholly posterior to the trigeminus and facialis foramina. There is said to be a pila prootica, but no prefacialis commissure in the specimens examined.

In *Polypterus*, the pituitary fossa is of my Type I. The posttrigeminus branchial-ray bar fuses with the dorso-lateral edge of the polar cartilage, is wholly postpalatinus in position and forms the lateral wall of the jugular canal. There is a prefacialis commissure and a trigemino-facialis recess. The trigeminus ganglion lies in a fossa in the hind wall of the orbit which seems to be the homologue of the trigeminus portion of the trigemino-pituitary fossa of the Selachii. The conditions in this fish thus resemble those in *Acanthias blainvillii*, excepting in that the rami palatinus and hyomandibularis facialis enter the jugular canal through one or two foramina in its mesial wall, the ramus palatinus running forward in the canal and the ramus hyomandibularis posteriorly. The nervi oculomotorius and profundus issue through a single foramen and de Beer considers this to indicate that there is no pila prootica in this fish, the band of cartilage that lies between this foramen and the trigeminus foramen and extends ventrally to the trabeculo-polar bar not representing this pila and being of secondary origin. In a 75 mm. specimen that I examined, the nervi oculomotorius and profundus issued through the same perforation of the cartilaginous wall of the cranium, but were separated from each other by a membranous bar which I considered to represent an unchondrified portion of the primitive cranial wall. The conditions here therefore resemble those

in *Scomber* and *Scorpaena*, where the basisphenoidal leg of the alisphenoid forms the anterior border of the trigeminus foramen and articulates ventrally with the antero-lateral edge of the prepituitary portion of the prootic bridge, the nervi oculomotorius and profundus lying in the line of fusion of these bones, but being enclosed in the anterior edge of the prootic. In *Acanthias* also the nervus oculomotorious may become enclosed in a foramen between the base of the cartilago antotica (pila prootica) and the anterior end of the parachordal (van Wijhe, 1922, p. 288). The basisphenoidal leg of the alisphenoid thus has the position of a pila prootica that has been greatly expanded anteriorly. The pituitary fossa is quite certainly primary.

In *Lepidosteus*, the pituitary fossa is of my Type I, but the conditions are complicated. The pituitary body presses the membranous floor of the primitive cranium downward until it meets and fuses with the perichondrial linings of the trabeculo-polar bars in a transverse line immediately posterior to the hypophysis. This forces the prootic bridge downward in a curved line and the cavum sacci vasculosi becomes a closed space. The lateral walls of this space are formed by the polar cartilages, the dorso-lateral edges of which fuse with the wall of the primitive cranium along the curved lines of the lateral edges of the prootic bridge. Anterior to this, the membranous floor of the primitive cranium fuses, on either side, with the lateral edge of the trabeculo-polar bar as far forward as the pituitary vein. There it arches upward over that vein, thus enclosing it in a foramen which lies between the cranial wall and the trabeculo-polar bar, the vein not perforating the primitive cranial wall at any point. The posttrigeminus branchial-ray bar, de Beer's lateral and post-palatinus commissures combined, is said by him to grow up in part from the trabecular plate and in part from the basal plate, the dividing line between them being marked approximately by the palatinus foramen. This would seem to indicate, according to my theory, that my branchial-ray bar, which fuses primarily with the dorso-lateral edge of the polar cartilage, has also fused, but secondarily, with the juxtaposed lateral edge of the prootic bridge. Anterior to this, the branchial-ray bar fuses with the lateral edge of the trabeculo-polar bar along the line of its fusion with the primitive cranial wall, but the descriptions do not definitely show how far forward this fusion extends. The foramen for the ramus palatinus facialis lies along the lateral edge of the trabeculo-polar bar, slightly anterior to the prootic bridge, and de Beer says that his lateral commissure arises in part anterior to this foramen. But however this may be, the branchial-ray bar fuses with the wall of the primitive cranium both anterior and posterior to the ramus palatinus, thus enclosing it in a canal which extends upward to the floor of the trigemino-facialis chamber. Immediately anterior to this, the lateral wall of the cranium is formed, according to de Beer, by the pila prootica, the pila being said to arise from the floor of the cranial cavity, which is here formed, on either side, by the trabeculo-polar bar. This fusion with the trabeculo-polar bar must however, according to my theory, be secondary, for the pila prootica lies definitely in the

primitive cranial wall, while the trabeculo-polar bar is of extracranial origin. The foramen for the nervus profundus lies slightly posterior to that for the oculomotorius, and de Beer says that the nervus profundus in embryos of this fish has become enclosed in the pila prootica. This pila must therefore extend from the trigeminus foramen to the hind edge of the foramen for the oculomotorius, thus corresponding to the band of cartilage that has similar relations to these nerves in *Polypterus* and which de Beer there considers to be of secondary origin. The pila prootica is said to lie between and separate the nervus trigeminus and the pituitary vein, and this is actually the case in this fish because of the secondary fusion of the pila prootica with the trabeculo-polar bar. But the pituitary vein nevertheless still lies definitely ventral and external to the wall of the primitive cranium, the pila lying definitely in that wall and the nervus trigeminus perforating the wall posterior to the pila and somewhat dorsal to the floor of the cranial cavity.

The trigemino-facialis chamber is bounded laterally by the branchial-ray bar. The outer one of the two membranes that close the incisura prootica has been completely broken down and the inner one has ossified, the trigemino-facialis chamber of this fish thus corresponding to the trigemino-facialis recess, the jugular canal and the trigeminus fossa of *Polypterus*.

In *Amiurus*, the pituitary fossa is a modified form of my Type I, the polar cartilages fusing throughout their entire extent with the overlying primitive cranial wall. The pituitary fossa is thus reduced to a small median space overlying the fenestra hypophyseos. The branchial-ray bars are not developed.

In the non-siluroid Teleostei considered in the above review, the pituitary fossa is of my Type II, but it differs markedly in certain respects from that in *Amia*. In all of these fishes the posterior portions of the trabeculo-polar bars are depressed in early stages of development to a somewhat greater extent than they are in *Amia*, these portions of these bars persisting in certain of these fishes, but being resorbed in others. The preclinoid wall lies at a certain distance anterior to the hind ends of the trabeculae, while in *Amia* it apparently lies between those ends. The internal carotid arteries, as they turn upward to enter the cranial cavity therefore do not perforate the preclinoid wall, as they do in *Amia*, running upward in a median vertical membrane which extends from that wall to the membranous pituitary sac. The myodome thus extends further forward in these fishes than it does in *Amia*.

In all of the non-siluroid teleosts, the myodome is separated into dorsal and ventral compartments by a horizontal myodomic membrane, the pituitary veins and external recti muscles lying in the dorsal compartment and the internal recti in the ventral one. Associated with these changes in the myodome, the innervation pattern of the recti muscles differs slightly from that in *Amia*.

The posttrigeminus branchial-ray bar arises from the dorso-lateral edge of the polar cartilage, first fuses with the lateral edge of the prootic bridge and then forms the lateral wall of the pars jugularis of the trigemino-facialis

chamber. The ventral portion of this bar forms the lateral wall of the middle portion of the myodome. Anterior to this bar the myodome is without a lateral bounding wall, excepting as it may be formed by the ascending process of the parasphenoid. A large opening is thus left which leads directly into the orbit and is the orbital opening of the myodome. This opening is bounded posteriorly by the anterior edge of the ventral portion of the branchial-ray bar, anteriorly by the basisphenoid, dorsally by the prepituitary portion of the prootic bridge and ventrally either by the parasphenoid or the trabeculo-polar bar (*Salmo*). The opening is therefore in no way a perforation of the primitive cranial wall, lying primarily between that wall and the trabeculo-polar bar. The lateral wall of the primitive cranium never descends ventrally below the lateral edge of the prootic bridge.

The mesial wall of the pars jugularis of the trigemino-facialis chamber is formed by the lateral one of the two walls that close the incisura prootica, this wall undergoing in *Salmo* ossification without previous chondrification. The floor of this chamber is said by both Gaupp and de Beer to be formed by the lateral edge of the prootic bridge, but as this bridge forms part of the primitive cranial wall it cannot extend laterally on either side beyond the ventral edge of the incisura prootica, the floor of the trigemino-facialis chamber thus probably being formed by an outgrowth of the primitive cranial wall.

The cranial wall immediately anterior to the trigeminus foramen is formed in the adult by the basisphenoidal leg of the alisphenoid, the leg of this bone thus having the position of a pila prootica which is said to be absent in embryos. The anterior edge of the prootic bone overlaps to a certain extent this leg of the alisphenoid and this part of the prootic is perforated in *Scomber* and *Scorpaena* by the foramina for the nervi oculomotorius and profundus, these foramina lying approximately in the line of fusion of the leg of the alisphenoid with the antero-lateral edge of the prepituitary portion of the prootic bridge. In some of my specimens of *Scorpaena*, these two nerves issued through a single foramen, the conditions in these fishes thus here resembling those in *Lepidosteus* and *Polypterus*.

At an early stage in the development of certain of these fishes, the membranous pituitary sac rests upon the dorsal surface of the trabeculo-polar bars and it may there be fused with the perichondrial linings of those bars, as it actually is in the 12 mm. specimen of *Sygnathus* described by Kindred, and in the adults of *Lepidosteus* and *Amiurus*. When, for some reason, the pituitary sac is lifted off the trabeculo-polar bars, it apparently pulls with it a superficial layer of the perichondria of those bars, thus forming the horizontal and vertical myodomic membranes. The pituitary veins and the external recti muscles retain their primitive relations to the horizontal membrane and hence lie dorsal to it. The internal recti muscles break down the prepituitary portion of this membrane and push backward beneath its postpituitary portion, thus forming the ventral compartment of the myodome. In accord with this, the horizontal membrane only extends posteriorly as far as the hind

ends of the ventral flanges of the prootics and is attached to these flanges at or near their ventral edges, and the internal recti muscles do not usually extend beyond this membrane. Remnants of the prepituitary portion of the horizontal membrane have probably been crowded into the median line and there form some part of the median vertical membrane that encloses the internal carotid arteries as they run upward into the cranial cavity.

In *Ceratodus*, the pituitary fossa is of my Type I and there is no prefacialis commissure, for the lateral one of the two membranes that close the incisura prootica has been completely broken down. The pretrigeminus and posttrigeminus branchial-ray bars have fused by their dorsal ends with the lateral wall of the primitive cranium, but their ventral ends retain their primitive attachments to the epimandibular (palatoquadrate), instead of shifting mesially on to the pharyngomandibular (polar cartilage). The upper part of the space between the otic process and the lateral wall of the neurocranium is the homologue of the trigemino-facialis chamber of *Amia*, the ventral portion of the space being the homologue of the lateropituitary space of that fish. The ascending and otic processes of *Ceratodus* are therefore the homologues, respectively, of the pedicel of the alisphenoid of *Amia* and the lateral wall of the trigemino-facialis chamber. Schmalhausen agrees with me in this, but de Beer considers these several structures analogous and not homologous, and in support of this contention he gives the following reasons, either one of which, if correct, would be fatal to my theory:

1. The course of the ramus palatinus facialis which is said to prove the absence in *Ceratodus* of the prefacialis, postpalatinus and lateral commissures.

2. The identity of the otic processes of *Ceratodus* and *Heptanchus*.

3. The difference in origin of these structures, the processes of *Ceratodus* being of viceral origin and the corresponding structures of *Amia* of cranial origin.

The ramus palatinus facialis is said to issue from the cranial cavity with the nervus trigeminus and the ramus hyomandibularis facialis, and not thereafter to be separated from those nerves by cartilage, this being considered to prove the absence of his prefacialis, postpalatinus and lateral commissures. The prefacialis commissure is actually absent, as explained above, because of the breaking down of the lateral one of the two walls that close the incisura prootica, this being as in *Amia* and *Lepidosteus*. Beyond this point the ramus palatinus runs downward internal to the otic process, thus having to that process the relations that it has to the postpalatinus commissure of *Amia* and *Lepidosteus*, and if the otic process were to shift its ventral attachment from the palatoquadrate to the polar cartilage, normal postpalatinus and lateral commissures, one or both, would arise. These commissures are therefore not absent, but simply not yet in place, and it is to be noted that the otic process lies between the nervus trigeminus and ramus hyomandibularis, thus already having to these nerves the relations of a lateral commissure.

The identity of the otic process of *Ceratodus* and the so-called otic process of *Heptanchus* is considered to be established indirectly in the following manner:

1. The so-called otic process of *Heptanchus* is the homologue of the metapterygoid process of the Holostei and Teleostei because of their similar relations to the efferent mandibular artery, that artery running upward postero-mesial to both processes.

2. These two processes are the homologues of the otic process of Amphibia, because in *Salamandra* and *Chryptobranchus* a delicate artery, which de Beer considers to form the dorsal end of the efferent mandibular artery, runs upward postero-mesial to the otic process of these Amphibia.

3. The otic process of Amphibia is the homologue of the otic process of *Ceratodus*.

The otic process of *Ceratodus* is therefore the homologue of the otic process of *Heptanchus* and hence also of the metapterygoid process of the Holostei and Teleostei. From this it follows that the otic process of *Ceratodus*, being the homologue of the metapterygoid process of the Holostei and Teleostei cannot be the homologue of the lateral wall of the trigemino-facialis chamber of those same fishes.

These conclusions would evidently be correct, if the premises all were, but there is considerable doubt as to this, for in embryos of *Ceratodus*, Greil (1913) shows the efferent mandibular artery running upward lateral and anterior to both the otic and ascending processes, and de Beer (1926 *a*) shows this artery in what are apparently similar relations to these processes in his fig. 69, p. 304, of an embryo of this same fish. If then the relation of this artery to the otic process is of such morphological importance, the otic process of *Ceratodus* is not the homologue either of the so-called otic process of *Heptanchus* or the metapterygoid process of the Holostei and Teleostei, and the delicate artery described by de Beer in *Salamandra* and *Chryptobranchus* does not represent the dorsal end of the primitive mandibular aortic arch.

The third objection to my theory, that the two processes of *Ceratodus* are of visceral and the corresponding parts of *Amia* of cranial origin has been discussed above and the facts as there presented certainly are favourable rather than unfavourable to my theory. Furthermore, if the polar cartilage is of visceral origin, as I maintain, no process arising from it could be of cranial origin.

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PALAIS CARNOLÈS,
MENTON, FRANCE.

December 26th, 1927.

ANATOMICAL NOTE

AN INFREQUENT DEVELOPMENTAL ABNORMALITY OF THE FOOT

By SYLVIA B. WIGODER, M.D.
Assistant Radiologist, Mercer's Hospital, Dublin

The cases of Pirie's dorsal astragulo-scaphoid bone that have been described in English medical literature are far from numerous. Indeed, Pirie himself, in the *Archives of Radiology* for 1919, only recorded eight. The following case and the radiograms showing this condition may therefore be of interest.

The patient, Anthony ..., aged 27, was sent to the X-ray department for a suspected tubercular lesion of the right ankle. He stated that twelve years previously, when he was fifteen, he had been struck on the dorsum of the right foot by an iron girder. The lateral radiogram of the foot revealed a small piece of bone in the astragulo-navicular articulation, and this was also faintly indicated in the radiogram taken in the anterior posterior view. The left foot showed no abnormality when radiographed for comparison. It might be said that the abnormality was the result of his old accident, but against this are the facts that:

(1) The shapes of the astragulus and the navicular bones were quite normal.

(2) The bony outlines were quite distinct and sharply defined.

(3) There was no sign of injury to the other bones, and a girder falling across the whole dorsum of the foot is unlikely to fracture, and cause no displacement of only a small piece of bone lying at an articulation.

(4) In a fracture of this duration one would expect either some callus formation, or else complete absorption of such a small fragment.

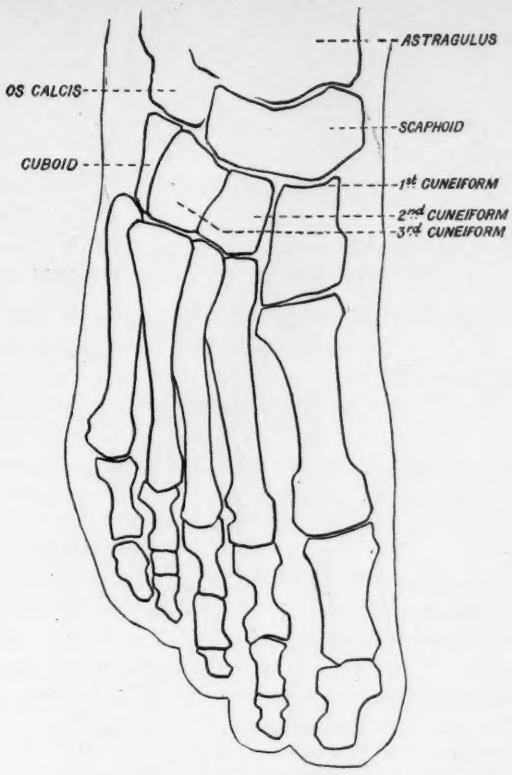
(5) A small fragment of bone lying in this position would possibly cause pain, and until six months ago the patient suffered no disability.

The other theory that it is the congenital accessory ossicle of Pirie is more probable, as it resembles published illustrations of this condition.

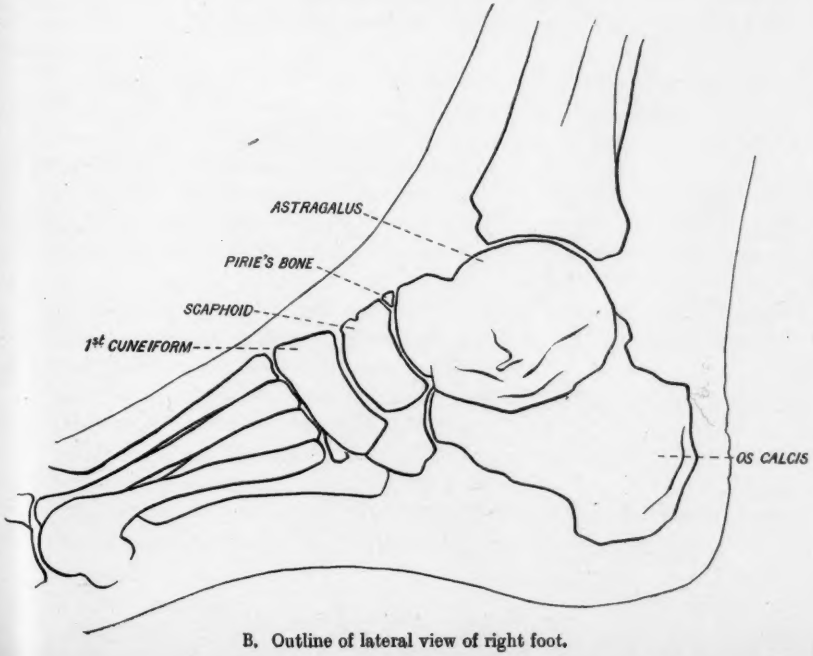
Had the condition existed in both feet, no doubt would have existed as to the diagnosis, but although developmental abnormalities are usually bilateral, this is not always the case. Cervical ribs are frequently found on one side only, and of eight cases in which Pirie found this bone, in one only was it bilateral. He does not state, however, if both feet were always radiographed.

It is of interest to note that the radiograms of the wrist in this case show sesamoid bones at the metacarpal joints of the thumb, index and little finger, and also at the inter-phalangeal joint of the thumb.

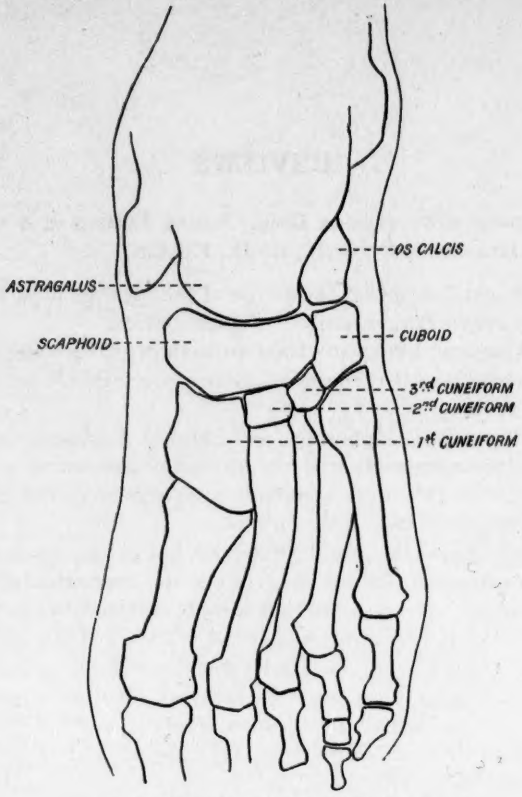
I wish to thank Dr Garratt Hardman, the radiologist to this hospital, and Mr Maunsell, the surgeon in charge, for permission to publish this case. To the former also my grateful thanks are due for his kind and valuable assistance.



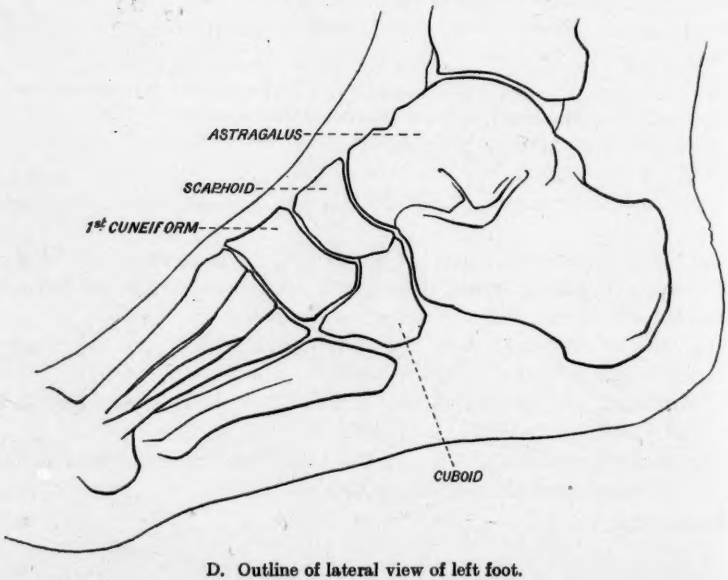
A. Outline of dorsal view of right foot.



B. Outline of lateral view of right foot.



C. Outline of dorsal view of left foot.



D. Outline of lateral view of left foot.

REVIEWS

Surgical Anatomy of the Human Body. Second Edition in 3 volumes. By JOHN B. DEARER, M.D., Sc.D., LL.D., F.A.C.S.

We cannot help feeling that the author of this gigantic work has sacrificed a great opportunity to the production of a mass effect.

Some 2168 pages and 480 plates there are in the three volumes, and although there is little or nothing that is original there is much that is unnecessary and even confusing.

The pointless mixing of Surface and Surgical Anatomy, with practical dissection, and even instruction in the method of preserving a brain, might perhaps be forgiven if the work were truly comprehensive. But unfortunately many important points have been omitted.

The text is large and the printing excellent, but the description can best be referred to as orthodox. Indeed, it gives one the impression of compilation rather than original expression. We were sorry to see the out-of-date hackneyed account of the Pelvic Fascia on page 559 of vol. III, and the omission of any reference to the lower lip of the Hiatus Semilunaris on page 386 of vol. II conforms too closely to the description given in most standard text books.

The Bulla Ethmoidalis is described as forming the dorsal bank of this river bed, but the ventral—formed by the uncinate process of the Ethmoid bone—is unmentioned. This detail may be considered unworthy of note but it is indicative of the slavish following of standard description pursued by the author.

Much space is allotted to surgical procedure, and many ambiguous statements are uttered, for example on page 40 of vol. I, "These conditions may cause compression of the Brain, symptoms of which coming on immediately after an injury to the head indicate *depressed* fracture."

The Ligation of Arteries in Continuity, one of the rarest of operations, is dealt with at great length, whereas there is neither description nor diagram of the Segmental Nerve Supply of Muscles, knowledge most vital to the diagnostician.

The plates for the most part are sound without being very helpful if we except some excellent diagrams of Fracture, but many are repeated and some so tortured with detail, that their clear outline is lost.

The book is colourless both figuratively and in fact, and not a single radiogram gladdens any of the three volumes.

Neither bone, nor Pyelogram, nor Barium filled viscus is portrayed in its natural surroundings by the medium of the X-rays.

Except as a monument of industry the work cannot be considered to have justified the time spent on it or the space allotted to it.

Travaux du laboratoire de recherches biologiques de L'Université de Madrid. Tome xxv, Fascicule 1er, 1927.

The present number of the published records of investigation in the laboratory of the veteran neurologist, Professor S. Ramón y Cajal, presents rather less than usual in the way of special interest to the neuromorphologist.

Of the four contributions it contains, only one, by Ramón y Cajal himself, is primarily anatomical. It deals with the anatomy and the possible connections of a fibre tract in the peduncular region of the brain stem called by the author the collateral motor pathway of the cerebral peduncle ("voie collatérale motrice du pédoncule cérébral").

This fibre system is specially evident in Rodents and is doubtless present in Mammalia generally. The author found it quite well developed in the cat. He had already described it, in 1900, in his publication dealing with the subthalamic pathways in Rodents. At that time the author was disposed to identify the system with one or other of the tracts which in the human subject enter Forel's field H 2. Now, however, he definitely gives up this view of its homology for the reason, among others, that no system corresponding to the field H 2 can be recognised in Rodents. For the present, therefore, he is content simply to recognise the tract in question as a system of descending motor collaterals taking origin from the longitudinal fibres of the basis pedunculi close behind the corpus Luysii. As such it forms a highly distinctive, and at first more or less compact, fasciculus, whose fibres pursue an arcuate course dorsally and then caudally above the region of the substantia nigra, beyond which its fibres become dispersed and intermingled with others of diverse origin.

The author expresses surprise that so clearly defined a fibre system should have failed to attract the notice even of those investigators who have given special attention to the brain of Rodents. He suggests that this may be due partly to the too exclusive study of transverse sections, which are little adapted to its demonstration, and partly to the fact that the method of Golgi has been insufficiently utilised in the study of this region.

The problem of the ultimate relationships of this prominent tract of motor collaterals will be followed up by the author if time and health permit.

Of the other papers, contributed by two of Ramón's pupils, one by Domingo Sánchez y Sánchez deals with the histological changes in the nerve centres of insects during metamorphosis, and the respective rôles of histolysis and phagocytosis in the reorganisation of these nerve masses.

The general conclusions are (*a*) that histolytic changes are primary and result from the influence of the circulating fluids, phagocytosis only following when degenerative change has already affected the constituent neurones: (*b*) that the destructive processes affect those ganglionic territories which correspond to the larval organs and functions unrepresented in the mature form of the animal: (*c*) that active histogenesis from the residual ganglionic

tissue results in the reorganisation of nerve centres modified and adapted to the activities of the metamorphosed insect.

The remaining two papers, by J. M. de Villaverde, embody the results of histopathological studies of the toxic effects of lead salts on the cerebellum and on the peripheral nerves, respectively.

Lehrbuch der Normalen Anatomie des Menschen. By Prof. SIEGLBAUER. Innsbruck. (Urban and Schwarzenberg, Berlin and Vienna.) 1927. Pp. 910, no figs. Price 21 marks.

This is an attempt at writing a systematic textbook of Anatomy devoid of illustrations with a view to its use in conjunction with a standard atlas of Anatomy such as the Toldt-Hochstetter or the Spalteholz. It is claimed that such a book can be handled by the student with facility. The various systems of the body are treated in order and the development of the various organs is described along with the gross anatomy. Such a book may be of use as a work of reference and for the preparation of formal lectures, but it is doubtful whether the student will undertake the work of cross reference involved in the use of a textbook and atlas conjointly.

Handbuch der Anatomie des Kindes. By Drs PETER, WETZEL and HEIDERICH. Zweiter Band, I. Lieferung. (Munich; Bergmann.) 1927. Pp. 154. Figs. 79. Price 24 marks.

With the rapid development of Pediatrics in Europe and America the need for a textbook of the Anatomy of the Child has become pressing. The present volume is the first part to appear and it deals with the urogenital apparatus and the organ of vision. The account of the urogenital system by Peter is a masterly one for it includes the gross and microscopic anatomy and a detailed account of the rate of growth which is of use to the experimental physiologist and the clinician no less than to the anatomist and pathologist. Thus for the kidney the variations in position with age, the relative proportions of cortex and medulla, the rate of growth in number and size of the tubules and glomeruli are tabulated. The pelvis and genital organs are treated with great detail and the histology of the bladder, descent of the testicle and variations in the form of the genitalia are figured in most useful fashion. There is an excellent table of the relative size of the constituent parts of the female organs from birth to adult life. The changes in the ovary and the process of atresia of the follicles are well illustrated.

The section dealing with the eye is well devised to meet the needs of the anatomist and clinician. The earlier stages of development of the retina are not described in detail but are figured from the eighth month of foetal life. Tables give the rate of growth of the eyeball and orbit and the results of Scammon are incorporated.

It is to be hoped that the remaining sections of this work will maintain the high standard and physiological outlook of this first part.

APPOINTMENTS

THE Editors of the *Journal* wish to keep a record of appointments secured by members of the Anatomical Society of Great Britain and Ireland. The accompanying list includes those made in recent years so far as they are known. The Editors cordially invite the co-operation of readers of the *Journal* to assist them in making this list complete and in keeping it up to date in future issues of the *Journal.*

J. BEATTIE. Assistant Professor of Anatomy, McGill University, Montreal.

D. M. BLAIR. Professor of Anatomy, King's College, London.

A. N. BURKITT. Professor of Anatomy, University of Sydney, New South Wales.

R. B. GREEN. Professor of Anatomy, University of Durham, College of Medicine, Newcastle-on-Tyne.

T. B. JOHNSTON. Appointed Editor of *Gray's Anatomy.*

TUDOR JONES. Lecturer in Embryology, University of Liverpool.

F. WOOD-JONES, F.R.S. Professor of Physical Anthropology, Rockefeller Foundation, University of Hawaii.

ALEXANDER LOW. Regius Professor of Anatomy, University of Aberdeen.

J. H. MULLIGAN. Demonstrator of Anatomy, St Thomas's Hospital Medical School.

E. P. STIBBE. Senior Demonstrator of Anatomy, University College, London.

C. M. WEST. Professor of Anatomy, University of South Wales and Monmouth, Cardiff.

H. H. WOOLLARD. Professor of Anatomy, The University of Adelaide, South Australia.

Anatomical Society of Great Britain and Ireland

PROCEEDINGS

November, 1927 *February*, 1928
May, 1928 *June*, 1928

RECORDED BY
R. J. GLADSTONE

EDITED BY
E. BARCLAY-SMITH

PROCEEDINGS OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND

THE Annual Meeting of the Society was held at the Middlesex Hospital Medical School on Friday, November 25th, 1927. Professor Elliot Smith, succeeded by Professor Fawcett, the newly elected President, occupied the chair.

Dr J. W. PRYOR, introduced by Sir Arthur Keith, read a paper on "The difference in ossification of the male and female skeleton."

By means of X-ray photographs he showed that ossification is inaugurated much sooner than has hitherto been supposed, and that ossific centres appear earlier in the female than in the male. The paper will be published in full in the *Journal of Anatomy*.

Professor ELLIOT SMITH remarked that the work of Mr Harris carried out at University College fully confirmed Dr Pryor's observations, and he drew attention to the importance of these results in the relation to the estimation of age of the Royal Mummies from Egyptian tombs.

Professor FRAZER commented on the medico-legal aspect of Dr Pryor's work, and raised the question of the condition of the bones, in pseudo-hermaphrodites. He regarded the appearance of ossific centres at an earlier stage in girls than in boys as indicating that the sexual hormones were active at an earlier period in females than in males.

Professor PATTEN suggested that the earlier fusion of the epiphyses of the long bones in the female as compared with the male was associated with the growth in length of the long bones coming to an end at an earlier age in women than in men.

Mr E. WOLFF read a paper on "A bend of the sixth cranial nerve, and its clinical significance."

He considered that palsy of the VIth nerve was not due to a simple longitudinal stretching of the nerve, produced by downward pressure on the cerebellum and pons Varolii, or to pressure of neighbouring arteries as has been supposed, but to pressure on the nerve where it forms a bend at the apex of the petrous portion of the temporal bone. He demonstrated the origin of the abducens nerve from the brain between the pons and the lateral part of the pyramid, and showed that it is attached to the pons for a few millimetres, and then runs upwards, forwards, and slightly outwards, between the pons and occipital bone, to pierce the dura mater below and to the inner side of the Vth nerve. Under the dura mater it courses almost vertically upwards on the posterior aspect of the apical part of the petrous temporal, and having arrived at the *sharp* upper border of this bone, it bends forward under the petrosphenoidal ligament of Gruber, and runs almost horizontally forward in the cavernous sinus. This portion of the nerve forms practically a right angle with the first part. In the sinus it is placed to the outer side of the carotid artery, to which it is held by communications from the sympathetic plexus.

Downward pressure of the brain towards the foramen magnum, such as may be produced by increased intracranial pressure due to tumour, will cause the origin of the nerve from the lower border of the pons to be carried downwards. This will produce pressure on the nerve at the bend where it passes over the sharp upper border of the apex of the petrous part of the temporal, with resulting paralysis of the external rectus muscle.

Miss IDA C. MANN read a paper on "The process of differentiation of the retinal layers in vertebrates," of which the following is an abstract.

A study of the developing retina in various animals representative of the vertebrates leads to the conclusion that a certain basal plan of differentiation can be traced throughout the phylum and that this is subject to individual modifications in different species. One can distinguish an underlying principle which remains unchanged, as well as an evolutionary scale of modifications superimposed on this.

From a study of the general principle it is apparent in every case:

(*a*) That the ganglion cells are the first to differentiate.

(*b*) That the amacrine cells are intimately associated with the ganglion cells and only secondarily separated from them.

(*c*) That the inner nuclear layer is a complex layer containing elements derived from both the primitive retinal layers (i.e. the inner and the outer neuroblastic layers).

(*d*) That the percipient elements themselves are the last to differentiate.

From a study of the secondary modifications it is apparent:

(*a*) That throughout phylogeny there is a tendency towards improvement of function by reduction in size and increase in number of the percipient elements in a given area.

(*b*) That supporting tissue differentiates relatively late in phylogeny, being only clearly recognisable in embryonic stages of animals above the fish.

(*c*) That abbreviation of stages can occur without modification of the general plan, such abbreviation usually taking the form of reduction in thickness of the non-nucleated layers in early stages.

Professor ELLIOT SMITH congratulated Dr Mann on the excellence of her demonstration and drawings. He was doubtful of there being a complete absence of Müllerian fibres in the retinae of fishes.

Professor LE GROS CLARK said that there was a considerable difference between nocturnal and diurnal animals as regards the lamination and thickness of the retinal layers.

Miss MARGARET M. WHITE described a case of Van Recklinghausen's disease, in which a generalised dermatitis was associated with left hemiplegia. There was an extensive subdural haemorrhage, and marked thickening of the nerves beyond the points where they pierced the dura mater. The cutaneous nerves often showed beaded thickenings. Non-pedunculated fibrous nodules were present on the skin, the largest of which was about 2 cm. in diameter, and there were areas of pigmentation on the thighs and arms. A detailed description of the case will be published at a later date in the *Journal of Anatomy*.

Professor Le Gros Clark made a preliminary communication on "An experimental study of the nature of the synovial membranes of joints."

Rabbits were used for the experiments. Under ether anaesthesia, the knee-joints were injected with ½ c.c. of 0·25 per cent. trypan blue in Ringer's solution under aseptic conditions. At variable times after the injection, the animals were killed. Smears were taken of the fluid found in the joint cavity. The suprapatellar pouch of synovial membrane with its walls was removed entire, thus preserving the synovial membrane where it comes into relation with bone, muscle, and tendon (quadriceps). The subsynovial pads of fat were also excised. The posterior pad, found at the back of the joint in close relation with the cruciate ligaments, was principally used for study because from its position it was protected from injury by the injecting needle, and the possibility of subsynovial extravasation of dye excluded. The pieces of tissue were washed in saline after removal, and placed in 5 per cent. formalin. They were prepared for paraffin sections in the usual way, the sections were cut at 10μ, and stained with Mayer's carmalum.

The exudate. The immediate response to the injection of 0·5 c.c. of 0·25 per cent. trypan blue into the knee-joints of rabbits is the outpouring of a copious exudate rich in polymorphonuclear leucocytes. Six hours after the injection a very occasional large mononuclear cell can be found in the exudate. These first arrivals of the large mononuclears contain no granules of dye. After 24 hours, large mononuclears comprise 5·5 per cent. of the cells in the exudate, after 36 hours, 9 per cent., after 48 hours, 40 per cent., and after 72 hours, 85 per cent. After the first day, more and more of these cells appear as typical clasmatocytes, until on the third day, most of the mononuclears, which now vary greatly in size, are heavily loaded with coarse granules of varying magnitude, in many cases packed very densely. At all stages, after the first day, occasional mononuclears were to be found with the remains of one, two, or three phagocytised polymorphs.

Reaction of lining cells of synovial membrane. Sections examined two hours and six hours after injection of trypan blue into the joint cavity gave no evidence of absorption of the dye. The mesothelioid layer of cells showed no appreciable change from the normal appearance. These cells contained no dye granules, and in the deeper layers no dye-containing clasmatocytes were found. This was also the case in the region of the reflection of the synovial membrane on to the quadriceps tendon (where histologically the mesothelioid layer appears to be deficient), and at the reflection of the synovial membrane on to the margin of the articular cartilage. On the other hand, in places where, during the injection, slight extravasation of the dye had occurred under the mesothelioid layer of cells into the subjacent subsynovial tissues (in the infrapatellar pad of fat), typical clasmatocytes, laden with coarse dark granules of dye, were readily to be found two hours after injection. These facts seem to indicate that the joint cavity is indeed a closed cavity, that it is lined by a continuous barrier which at first prevents the diffusion of solutions of trypan blue into the subsynovial tissues, and that there can be no question of the loose connective tissue spaces abutting directly upon the joint cavity. After 12 hours, absorption of the dye is found to be taking place rapidly. From the manner in which the dye is stored in the cytoplasm, two types of cells are to be recognised on the surface of the synovial membrane: (1) mesothelioid cells which have taken up the dye in fine discrete granules, sometimes only to be seen in the neighbourhood of the nucleus, forming a perinuclear

ring, and sometimes scattered evenly throughout the cell-body, and (2) typical clasmatocytes which have stored the dye in coarse granules of varying dimensions often collected into irregular clumps. The mesothelioid cells show signs of active proliferation, many have rounded up into an irregular cuboidal form, and some are to be seen projecting from the surface as though in the process of becoming detached. The clasmatocytes containing dye are at first confined to the surface of the synovial membrane or immediately beneath the mesothelioid layer. After 24 hours, clasmatocytes are found at deeper levels, extending in among muscular and capsular fibres. Forty-eight hours after injection, the picture shown by the sections of the synovial membrane becomes more confused. The mesothelioid cells become swollen and irregular in contour and can frequently be observed lying free on the surface of the membrane either singly or in groups of four or five desquamated cells. Their cytoplasm takes on a vacuolated appearance, the nucleus becomes eccentric, and the dye is taken up in much larger quantities. In these later stages it is not always possible to differentiate between typical clasmatocytes and mesothelioid cells by reference to the quantity of dye stored in the cytoplasm, although in many places the distinction between the two types is still quite evident. That the mesothelioid cell can assume phagocytic properties under the influence of stimulation seems assured by the following experiment. A rabbit was injected intravenously with 0·5 per cent. trypan blue on five alternate days. Twenty-four hours before the last injection, ½ c.c. of laked blood was injected into the knee-joint. In this case, the mesothelioid cells had only taken up the dye in very sparse, fine granules, while typical clasmatocytes were present in the deeper subsynovial tissues. Mesothelioid cells were found, however, in the evident process of becoming detached from the surface with 2 or 3 erythrocytes in their cell-bodies. These experiments do not finally decide whether the mesothelioid cells become set free in the exudate to form free mononuclear cells, which are capable of maintaining their phagocytic properties in a manner comparable with true clasmatocytes, but that this actually occurs seems very probable. Seventy-two hours after injection the picture appears less confused. In many places, the surface of the synovial membrane is covered by an unbroken zone of mesothelioid cells which contain but few granules of dye of small size; deep to these are seen crowds of typical clasmatocytes well filled with trypan blue. This suggests that, in general, the identity of the mesothelioid cells is maintained under the influence of the stimulus provided by the injection of the dye. It may be noted that absorption of the dye is not nearly so evident in the region of the suprapatellar pouch as it is over the surface of the fatty pads. The sections of the synovial villi provide no support for the suggestion that these structures are especially concerned in the process of absorption from the synovial cavity.

Reaction of cartilage cells. So far as could be ascertained, the cells of the articular cartilage did not take up the dye under the conditions of the experiments. The cartilage cells on the deep surface of the quadriceps tendon contained fine granules of dye after 24 hours, and these became more conspicuous at later stages. The dye appeared to be taken up in a manner precisely similar to the storing of the dye by the synovial mesothelial cells, which seems to provide further evidence that cartilage cells are modifications of the synovial mesothelioid cells.

In conclusion, it is believed that a joint cavity is to be regarded functionally as a closed sac lined, except at points of mechanical pressure, by a layer of

cells modified to form a true mesothelial lining. These cells react towards trypan blue in a manner comparable to the reaction of other mesothelial cells, especially those of the arachnoid membrane. The *whole* mesothelial lining appears to be concerned in the absorption of the dye from the joint cavity. Although these mesothelial cells may, under the influence of irritation, become transformed into cells indistinguishable from true clasmatocytes, it is maintained that they cannot under normal conditions be regarded as clasmatocytes (as Petersen suggests—*Histologie und Mikroskopische Anatomie*, München, 1924, p. 256) for the reason that they do not at first react towards trypan blue in the way in which typical clasmatocytes react.

The absence of a mesothelium over regions exposed to pressure, such as the intra-articular menisci, may be emphasised in view of the fact that current text-books of anatomy commonly describe intra-articular cartilages, ligaments and tendons as being covered by a reflection of synovial membrane.

Professor Brash enquired whether Professor Le Gros Clark had found any evidence of secretion of synovia by the synovial villi.

Professor Barclay-Smith said that synovia was not a definite secretion but was a complex fluid in which the detritus of cartilage played an important part.

Professor Yeates said he believed that the cavities of the body, including the synovial cavities, are originally continuous with and are derived from the coelom.

Professor Blair concurred with the statement that the synovial membrane does not cover the semi-lunar cartilages, but lines the capsule.

The President remarked that it is generally admitted now that the synovial membrane is not present over pressure points, such as the menisci and articular surfaces.

Professor Le Gros Clark in reply said that his sections did not indicate that the synovial villi were concerned more than any other part in absorption.

Dr Hunter read a paper on "Some facts involved in the development of the ascending colon."

He stated that when the colon is withdrawn from the umbilical coelom, it passes obliquely from the right iliac crest upwards and to the left to the splenic flexure, and that in the situation where the colon crossed the duodenum, an adhesion occurs. This adhesion forms a fixed point in the changes which result in the definitive ascending colon. The segment between the adhesion and the caecal anlage forms the whole of the ascending colon and that part of the transverse colon between the duodenum and the hepatic flexure; the segment to the left the remainder of the transverse colon. The mesentery of the gut in relation with the ascending colon disappears when the colon rotates on its long axis and brings it into close apposition with the dorsal peritoneum.

Professor Frazer said that an actual rotation of the ascending colon occurs and as a result the anterior taenia coli becomes postero-lateral. The colon is attached between two fixed points. As the liver retreats in an upward direction away from the iliac crest, there is an elongation of the ascending colon.

DEMONSTRATIONS.

E. P. STIBBE for W. H. WOOD and for F. DAVIES and E. P. STIBBE.

(1) Anomaly of superficial thenar and hypothenar muscles.

This case showed complete inter-crossing of the flexor brevis muscles of the pollex and fifth digits.

Flexor brevis pollicis: the outer head arises from the scaphoid and trapezium, and from the pisiform by a long independent tendon. The inner head continuous across proximal part of palm with opponens digiti quinti.

Flexor brevis digiti quinti: arises from the pisiform and from the hook of hamate, also by a wide head from the opponens pollicis.

These inter-crossing origins were large, musculo-tendinous and independent; they were on the same plane as and partly superficial to the anterior annular ligament.

Attention was drawn to the fact that most normal specimens show indications of this tendency to crossing of fibres, and that many of the fibres of the anterior annular ligament decussate. These appearances fitted in best with McMurrich's views of the derivation of the thenar and hypothenar muscles, namely from a primitive superficial flexor layer.

(2) Origin of the plantaris muscle.

Diagrams and a specimen were shown to demonstrate the usual origin of the plantaris—namely:

(i) From the lateral edge of the patella and the lateral patellar ligament, by retinacular fibres.

(ii) From the back of the capsule of the knee-joint under cover of the edge of the lateral head of the gastrocnemius.

(iii) From the popliteal surface above the lateral condyle, and a small origin from the lateral supracondylar ridge.

The first two origins are frequently large, and can be traced in the majority of cases.

(3) Vesico-vaginal fistula with separate anal and vaginal openings.

A sagittal section of the pelvis of a female aged 46, from the dissecting room of the University of Liverpool was shown.

Rather more than the lower half of the vagina has no posterior wall and communicates so freely with the rectum that the rectum and vagina open into a large cloacal space. This space however has two openings to the exterior, anal and vaginal, consequently external inspection would not suggest any anomaly. The upper half of the recto-vaginal septum is normal, and has a free arched and slightly thickened lower edge. The uterus is very small and its walls much thinned out.

The uterus and vagina, as well as the rectum and "cloaca," were packed with large quantities of impacted faeces.

The vagino-vesical and vagino-urethral septa are normal.

The urethra and vulva are also normal.

Histological study unfortunately did not show recognisable epithelium and did not give sufficient information to justify an opinion as to whether the condition was pathological.

If the condition be not pathological it is exceedingly difficult to understand the normal external openings.

(4) Reduced first rib.

A specimen was shown in which the first thoracic rib on the right side fails to reach the sternum by nearly three inches, and articulates instead with a large tubercle on the inner edge of the second rib. When first noticed in the dissecting room it was taken for a cervical rib; it articulates however with the first thoracic vertebra, there are eleven ribs below it, and the thoracic and lumbar regions are normal in all other respects. The second costal cartilage articulates with the manubrium sterni *on both sides* in the position usually occupied by the first. The first piece of the body of the sternum is fused with the manubrium, and the angle of Louis is at the junction of the first and second pieces of the body. The distal end of the first right rib is joined to the sternal angle by a well-marked tendinous band, and the scalenus anticus is inserted into this band; the scalenus medius is inserted into the first rib behind a well-marked groove for the artery and inner cord of the plexus, and it "overflows" on to the second as a poorly differentiated scalenus posticus; (this is often found when the first rib is normal).

The brachial plexus receives a contribution from the second thoracic nerve.

References were made to cases reported by Struthers 1874, Macphail 1903, and Keith and Hertzlet 1895; the present case agrees in essentials with Keith and Hertzlet's.

For F. Davies and E. P. Stibbe.

Anomalous fissure of right lung.

A right lung taken from an adult in the dissecting room of University College, London, was shown. The general shape and relations of the lung are normal. Oblique and transverse fissures are placed in usual positions, but the transverse fissure has a backward prolongation, which extends from the junction of the transverse and oblique fissures horizontally backwards to the posterior border of the lung, but does not encroach on to its medial surface. This extra fissure is complete in its whole extent, that is, it cuts right through the lung-substance as far as the root.

Dissection by Dr Davies revealed a large dorsal bronchus distributed to the portion of lung between the oblique fissure and the backward prolongation of the transverse fissure. The ventral bronchi are the usual large "first ventral" distributed to the middle lobe, followed by a tuft of smaller bronchi to the lower part of the lower lobe.

It is proper to call this an extra lobe, since it has a definite bronchus. The fact that it is not completely isolated posteriorly does not discount this assumption since the normal middle lobe is also not completely cut off from the upper lobe anteriorly, and this is quite a common condition. The dorsal bronchus to the extra lobe is present in normal lungs, supplying the upper part of the lower lobe; but it is usually smaller than in this case where it appears to have taken on extra importance as the supply of a definite lobe.

Reference was made to Gillespie, Millar and Balkin with summary of literature (*Anat. Rec.* 1916, vol. xi).

Also the condition appears to be normal in certain animals, as sheep, notoryctes, goat (Museum of Royal College of Surgeons, specimens 1131 F, 1130 D, 1131 E).

E. P. Stibbe.

Divided occipital condyle.

A skull showing complete division of the right occipital condyle into anterior and posterior halves. The posterior half does not occupy its usual position, but has apparently shifted into the hollow below and behind the jugular process of the occipital bone. The skull differs from similar specimens in that the latter usually have a complete condyle, with an *additional* articular process projecting down from the jugular part of the occipital bone. Unfortunately the atlas is not available, and it is only possible to conjecture the cause of the condition. The right mastoid process is flattened from side to side and elongated antero-posteriorly, but the mastoids of normal skulls are often asymmetrical. Careful measurement of various dimensions on the two sides of the skull and especially of the face show complete symmetry.

The skull is the property of Miss Winner of University College, London, who has kindly lent it for exhibition.

Professor Wright said that he had frequently seen the abductor pollicis continuous at its origin with the extensor ossis metacarpi pollicis.

Mr Harris remarked on the similarity of the muscles of the thumb to those of the great toe both arising from the post-axial border of the limb.

Professor Wright drew attention to the common mistake of speaking of the "sternal angle of Louis" as the angle of Ludwig.

Professor Elliot Smith said that the anomalous rib might be explained on the supposition that there was an atrophy of the anterior part of the first thoracic rib.

Mr Harris suggested the possibility of the sternum having slipped downwards, as an explanation of this and similar cases.

Dr Stibbe said that there was no evidence of the brachial plexus being post-fixed.

In the discussion on the additional lobe of the right lung—

Dr Gladstone said that he had recently seen a similar case, and considered that the abnormal fissuration of the lungs may have been produced secondarily.

Professor Frazer agreed with the opinion expressed by the former speaker, and said that he believed the fissures were produced as an adaptation to the movements of the thoracic wall.

Mr Harris referred to the frequency of broncho-pneumonia affecting the middle lobe of the right lung in children, and thought that there might be some relation between this and the mobility of the middle lobe.

Mr C. P. G. Wakeley with Dr R. J. Gladstone presented a paper which was taken as read, on "The relative frequency of the various positions of the appendix vermiformis, as ascertained by an analysis of 5000 cases."

The position of the appendix was noted in the operating theatre, post-mortem room, and dissecting room, and the observations include the usual cases which are likely to be met with in surgical practice.

Some practical points in connection with the investigation are of importance, namely:

(1) The position of an abscess in appendicitis is most likely to be determined by the original position of the appendix.

(2) The liability to the occurrence of mesenteric thrombosis leading to portal pyaemia in the splenic, or post-ileal position of the appendix.

(3) The secondary connection of the lymphatic vessels of the appendix

with those of the ovary in the descending or pelvic position of the appendix. The following table shows the percentage frequency and numbers of the cases recorded:

Position of the appendix caeci	No. of cases (5000)	Percentage frequency
Anterior, or pre-ileal	47	0·94
"Splenic," or post-ileal	25	0·5
"Pelvic," or descending, near to or hanging over the brim of the pelvis	1606	32·11
"Subcaecal," beneath the caput caeci	101	2·02
Post-caecal and retrocolic	3219	64·38
Ectopic	2	0·04

FEBRUARY, 1928

AN ordinary meeting of the Society was held on February 3rd, 1928, at Guy's Hospital Medical School, the President, Professor Fawcett, being in the chair.

Professor T. B. JOHNSTON exhibited:

(1) A cast of the roof of the mouth, showing a median cleft involving the upper lip and premaxilla. The nasal septum was represented by a faint ridge only.

(2) Specimens showing transposition of the large vessels of the heart.

An account of these anomalies will be submitted for publication in the *Journal of Anatomy*.

Professor F. G. PARSONS showed a series of illustrations of English skulls, each illustration being the average of a large number of observations.

The series was intended to show the great increase in height of the modern English head, and had been prepared in order to illustrate a discussion on the evolution of head shape which Professor Parsons was to open at the Royal Anthropological Institute on February 14th.

Professor J. E. FRAZER read a paper on "The development of the region of the isthmus rhombencephali," which will be submitted for publication in the *Journal of Anatomy*.

The origin of the fourth cranial nerve, from two nuclei, namely a small homolateral nucleus and a large contralateral nucleus was discussed; it being supposed that the homolateral nucleus has undergone diminution, the contralateral increase in size.

Professor BARCLAY-SMITH compared the condition to the uncrossed and crossed fibres of the pyramidal tracts, and the anterior commissure of the spinal cord.

Professor FRAZER pointed out that the fourth cranial nerve differs from others, in the fact that normally it is functionally associated with the IIIrd nerve.

A discussion on Anatomical Nomenclature was opened by Professor T. B. JOHNSTON. He drew attention to the importance from the student's standpoint of having names which should be informative, and also the disadvantage of having several names for the same object. He also suggested that a certain number of unsatisfactory names should be eliminated. He further proposed that new terms should be introduced when the existing terms do not convey a definite meaning.

The PRESIDENT read a paper on "The primordial cranium of Gerbillus (Jerboa)." He demonstrated the chief points in the development of the cranium of Gerbillus, and incidentally pointed out the main features in the development of the human sphenoid bone. The paper will be submitted for publication in the *Journal of Anatomy*.

Professor LE GROS CLARK read a paper on "The brain of the Macroscelididae," which will be submitted for publication in the *Journal of Anatomy*.

Mr A. R. Thompson gave a demonstration on "Some artificial changes in post-mortem bones." These changes he had induced by:

(1) The growth of roots of plants introduced into foramina, and fissures of bone.

(2) The action of heat.

(3) Rolling of bone, imitating the action of sand in a river producing attrition. The post-mortem changes could be distinguished from the changes induced by disease, by the absence of any indications of reaction or repair.

Mr Harris pointed out that in order for vegetable life to live on animal life, the animal tissue or matter, e.g. glue, must first be converted into a soluble form before the plant can make use of it.

Professor Blair mentioned the effect of wear and tear on a plaster model of Robert Bruce, which simulated the effects of syphilitic disease. Another model which had not been worn was unaffected.

Dr G. W. Nicholson read a paper on "Examples of heterotopic tissues." This will be submitted for publication in the *Journal of Anatomy*. He drew attention specially to the formation of bone in scar tissue, and to the growth of teratomata.

Professor Parsons drew attention to the early stages of ossification being degenerative, and attended by calcification. With the appearance of osteoblasts and blood vessels, the degenerative process is changed into an active process of growth.

Mr Harris said that in children suffering from scurvy-rickets, red marrow was absent from the shafts of the long bones, there being nothing but yellow marrow. If the child was put on a blood-forming diet, new bone and new marrow was laid down without there being any attempt to remove the gelatinous tissue.

Professor Frazer, referring to the growth of teratomata, said that certain cells retain their potentiality to produce other tissues—under ordinary circumstances the tendency is for normal development; occasionally abnormal development may occur.

Dr Nicholson in replying said that changed conditions produce a changed direction of growth and a reaction takes place.

Mr B. G. Scholefield demonstrated "A case of craniopagus parietalis," which will be submitted for publication in the *Journal of Anatomy*.

MAY, 1928

AN ordinary meeting of the Society was held on Friday, May 4th, 1928, at the Medical College, St Bartholomew's Hospital, the President, Professor Fawcett, being in the chair.

Professor LE GROS CLARK exhibited a microcallosal brain from a woman aged 41 who had been in the Surrey County Mental Hospital since the age of 11, suffering from idiocy. The convolutional pattern of the cerebrum was normal except that the callosomarginal sulcus was shortened in correspondence with the abbreviation of the corpus callosum. The latter measured 31 mm. antero-posteriorly. Emphasis was laid on a curious anomaly in the blood supply of the thalamus. The anterior cerebral artery was traced along the dorsal aspect of the corpus callosum, and at its caudal extremity was found to give off a large branch which passed forward in the velum interpositum to supply the choroid plexus, thus taking the place of the posterior choroidal branch of the posterior cerebral artery. Three well-marked twigs were seen running into the substance of the anterior tubercle of the optic thalamus. This point was regarded as of especial interest in view of the fact that the anterior cerebral artery is generally regarded as the olfactory artery of the brain. A search for evidence revealed no embryological or phylogenetic explanations to account for the vascular arrangement described.

Dr G. SCOTT WILLIAMSON and Miss I. PEARCE read a paper entitled "Thyrothymic connections," which will be submitted for publication in the *Journal of Anatomy*.

Professor FRAZER commented on the supposed connection of the thymic sac with the thyroid gland, and doubted whether the cavities described by Dr Scott Williamson in the fish correspond to the thymus of mammals.

Mr HAROLD EDWARDS showed the following cases of congenital anomalies of the urinary tract.

1. Unilateral kidney of the discoid variety.

The specimen was obtained post-mortem from a male child nine days old. There was no kidney on the left side; on the right side, rather low in position, lay the specimen described. The kidney is circular in outline, and possesses two pelves which face forwards, and two ureters. The right ureter pursues a normal course, but the left crosses the mid-line to open into the bladder at the normal site. The posterior surface of the kidney is uniformly smooth, and shows nothing to suggest two separate organs. Pyelography, however, demonstrates the presence of two independent kidneys, the right being the larger, and forming quite two-thirds of the whole.

2. Congenital deficiency of one kidney, with hydronephrosis of the other.

The specimen was obtained post-mortem from a male child aet. nine weeks, and consists of the whole urinary tract. The right kidney is represented by a minute mass containing three or four very small cysts. The corresponding ureter is patent for a short distance at its upper end only. It is attached to the bladder wall in the normal situation but there is no trace of a ureteric opening inside the bladder. The kidney on the left side is large and its calyces are distended. There is very little kidney tissue remaining. The ureter of this

side is dilated and tortuous. It opens normally into the bladder, the orifice admitting a probe with ease. Near the expected site for the right ureteric orifice is a sessile mass of tissue, attached to the bladder wall. This, on first opening the bladder, was found to lie in the internal meatus, and it seems probable that this mass is the direct cause of the obstruction which caused the dilatation of the left kidney and ureter. This mass is clearly of developmental origin, though it is not clear in what manner, and to serve what purpose, it has arisen.

3. Aberrant accessory ureter.

A description of this specimen will be published *in extenso* in the *Journal of Anatomy*.

Mr H. A. Dunlop demonstrated a model showing the origin of a right apical bronchus from the trachea. The model had been reconstructed in wax by the Born method from a human embryo 6 cm. in length. A full description of the case will be published in the *Journal of Anatomy*.

Dr E. P. Stibbe exhibited the following specimens:

(1) Right aortic arch.
(2) Tracheal diverticulum.
(3) A skull showing large parietal foramina.
(4) A skull showing exaggerated grooving of the temporal region.
(5) An abnormal thenar muscle.
(6) A specimen showing enlargement of the diploic veins to form a collateral circulation in a case of obstruction of the superior sagittal sinus.

Mr A. J. Cokkinis read a paper on "The collateral circulation in the territory of the mesenteric vessels."

He showed that the circulation in the vessels of the intestine is not as is usually supposed "terminal" in character and that free anastomosis of neighbouring vessels occurs; he also showed that the arterioles on reaching the intestine from the mesentery pass to one or other side of the gut, and do not usually bifurcate into two branches, one of which passes on one side of the intestine and the other on the opposite side.

The paper will be published *in extenso* in the *Journal of Anatomy*.

Dr R. J. Gladstone demonstrated:

(1) A case of axillary mamma in a male.
(2) Models of the thoracic and abdominal viscera of a 9 mm. human embryo.

Descriptions of these will be submitted for publication in the *Journal of Anatomy*.

Professor Frazer enquired whether the model of the heart showed any sign of there being a septum secundum. He also commented on the large vitelline vein, which runs freely in the coelomic cavity from the umbilical cord to the duodenal region, where it joins with the superior mesenteric vein to form the portal vein. He stated that it persists for a considerable period, but finally disappears.

Dr Gladstone in reply said the specimen showed no indication of a septum secundum.

Professor D. M. Blair gave a communication on behalf of Dr J. A. Bingham and himself on "The nerves to the arteries of the human leg."

Through the kindness of Mr Duff, Surgeon to the Glasgow Royal Infirmary, an opportunity was given of examining the condition of the nerves to the main arteries of a leg amputated through the upper third of the thigh thirty-five days after periarterial injection of alcohol in the upper part of Hunter's Canal. The vessels were dissected out *en bloc* and preparations stained supravitally with methylene blue, with silver nitrate by Ranson's method, and with haemalum and eosin. Extensive degenerative changes in the arteries with much calcification in the tunica media prevented study of the finer arrangements of the vascular nerves, but the following points were established.

The main nerve trunks on the femoral artery were identifiable by dissection with a binocular microscope but showed no properly staining axons—they appeared to have undergone complete degeneration. Two or three small nerves with normal axons ran in upon the vessels in Hunter's Canal. These incoming nerves in part divided into finer bundles of fibres entering the main arterial nerve trunks. In one instance an incoming nerve was almost completely distributed upon a muscular branch of the artery arising immediately distally. In the popliteal space was found so large an accession of nerve fibres to the arteries, that the lower part of the popliteal artery and the anterior and posterior tibial arteries had an abundant supply of nerves with well-stained axons, in striking contrast to the appearance of the femoral artery. Sections of the posterior tibial artery showed both normal and degenerated nerve fibres in its wall. No degenerated fibres could be made out on the peroneal artery. The condition on the anterior tibial artery in this respect was not accurately ascertained. All the incoming nerves had a similar composition—chiefly fine medullated fibres, with a few large medullated fibres and a considerable number of non-medullated fibres. This study gives experimental confirmation in man of some of the results obtained by Woollard in animals (*Heart*, vol. XIII, 1926).

In a specially undertaken naked-eye dissection of a normal leg, no nerves were found running to the femoral artery in Scarpa's triangle, but two fine twigs joined the artery from the saphenous nerve in Hunter's Canal. A much richer supply of nerve twigs from the lower end of the great sciatic nerve and its internal popliteal continuation went to the popliteal artery just above its bifurcation and to the commencement of the anterior and posterior tibial arteries, more especially to the posterior tibial. Further twigs from the posterior tibial nerve went to the posterior tibial artery in the calf of the leg. Care was taken to trace the incoming vascular nerves definitely into the arterial adventitia. These findings confirm those in the experimental limb and are in general agreement with the results of Potts in dissections of the nerves to the arteries of the leg (*Anat. Anz.* vol. XLVII, 1914).

This work demonstrates the impossibility of interfering with all the vasomotor nerves of the leg by any periarterial operation in the upper part of the thigh—the supplemental supply from the ordinary nerves of the limb is left untouched.

The observation made on the nerve supply to the muscular branch of the femoral artery, coupled with the apparent absence of degenerated nerve fibres on the peroneal artery (usually an almost purely muscular vessel) while degenerative nerves were traceable on the posterior tibial artery (a "mixed" muscular and cutaneous trunk), suggests that possibly the incoming nerves in the limb are chiefly concerned with the vascular supply to the muscles.

SUMMER MEETING, 1928

THE summer meeting of the Society was held at the University of Manchester on Friday, June 22nd and Saturday, June 23rd, 1928. The President, Professor Fawcett, occupied the chair.

Professor LE GROS CLARK gave a communication on the optic thalamus of tupaia. The paper will be published in full in the *Journal of Anatomy*.

Professor ELLIOT SMITH read a paper on "The optic connections in the brain, and the need for a revision of the traditional description of this in the current text-books of anatomy."

He drew attention to the recent work by Brouwer, Minskowski and Woollard on the course of the nerve fibres of the optic tract, and of the representation of the retina in the lateral geniculate body, which according to Brouwer receives over 90 per cent. of the optic nerve fibres; whereas no fibres from the retina reach the superior colliculus, and it is very doubtful whether any reach the pulvinar of the optic thalamus. With the evolution of binocular vision revolutionary changes have been effected in every part of the visual system of man and his nearest allies. In mammals a transference has taken place to the neopallium of functions which in all other vertebrate animals are carried on in the mid-brain, and other lower centres. The experiments of Magnus have shown that the optic righting reflexes are not acquired until binocular vision is developed. With the acquisition of binocular vision (in mammals such as the cat or monkey) the fibres of the optic tract become rearranged. The fibres from the lateral part no longer cross to the opposite side but become so connected with the same side as to bring into connection the terminations of fibres coming from the medial side of one retina with the lateral side of the other. In binocular vision these necessarily so act together as to merge in consciousness the two images of one object.

The development of the macula lutea in the retina (monkeys and man) has brought about further changes in the brain. In the lower types optic fibres ending in the thalamus are connected with the awareness or consciousness of vision, and those ending in the superior corpora quadrigemina with such unconscious functions as the reflex actions of the eye muscles, and the general musculature of the whole body.

In mammals the lateral geniculate bodies for the first time in the vertebrate series emit a large strand of fibres (optic radiation) to provide a path for visual impulses to the cerebral cortex. According to Allen this process is not complete in the rabbit; its cerebral cortex controls the movements of the head, forelimbs and body, but the control of the hind limbs is still retained by the mid-brain. In most mammals however the transference of motor control to the cortex is complete.

In monkeys and man the macular fibres form more than one-third of the optic nerve and there is added to the geniculate body a new formation, a macular receptive mechanism. With the atrophy of the quadrigeminal fibres of the optic tract, and the sudden increase in the geniculate connection in monkeys and in man, practically the whole, more than 90 per cent., of the optic nerve fibres go to the lateral geniculate body. But with the enormous increase of the latter the body loses much of its autonomy. Its ventral nucleus

which in other vertebrates controls the quadrigeminal body has atrophied in the primates. In its place the cerebral connection is still further strengthened. The geniculate body becomes more and more an intermediary between the retina and the neopallium, and almost the whole function of visual perception becomes concentrated in the visual cortex.

Professor LE GROS CLARK concurred with Professor ELLIOT SMITH in considering that the time had come when the recent experimental work of Brouwer and Minskowski should be recorded in the text-books of Human Anatomy. He also alluded to the connection of the pretectal nucleus, with the lateral geniculate body, and the absence of any fibres connecting this with the cortex.

Dr J. BEATTIE read a paper on "The sympathetic nervous control of the heart," which will be submitted for publication in the *Journal of Anatomy*.

The PRESIDENT demonstrated methods for the identification of separate cervical and lumbar vertebrae, an account of which will be published with illustrations in the *Journal of Anatomy*.

Dr J. M. YOFFEY read a paper on "The essentials of haemopoiesis as seen in fishes," which is to be submitted for publication in the *Journal of Anatomy*.

Professor D. R. DOW and Dr H. J. R. KIRKPATRICK showed lantern slides and specimens of herniae in the region of the duodenum. Left duodenal hernia took place into the fossa of Landzert, and right duodenal hernia into the fossa of Waldeyer. The anatomy of these fossae was mentioned, and it was pointed out that the anterior boundary of the neck of a left duodenal hernia was formed by a fold of peritoneum containing the inferior mesenteric vein and the ascending branch of the left colic artery. The first case shown was one of a left duodenal hernia of moderate dimensions, which contained the first 39 inches of the jejunum. There was also present a carcinoma of the pylorus which caused pressure on the portal vein, with consequent enlargement of the inferior mesenteric vein, and it was suggested that in this way undue prominence was given to the anterior boundary of the mouth of the fossa of Landzert, and a possible explanation of the occurrence of the hernia was available. The second case of left duodenal hernia which was shown, presented more difficulty in diagnosis. When the abdomen was opened a thick layer of peritoneum was met with, and it completely concealed the small intestine, caecum, ascending colon, descending colon, and pelvic colon. It proved to be the anterior wall of a large hernial sac containing nearly the whole of the small intestine, and overlapping the above-mentioned parts of the large intestine. Another slide showed an X-ray picture of a duodenal hernia, the diagnosis of the condition was made in this case by means of a radiogram before operation. Views on the formation of duodenal herniae were discussed. Consideration was given to the theory of Andrews, viz. that they were the result of inclusions of intestine behind the peritoneum, due to faulty rotation of the large intestine and its mesentery during development, but as the condition was not stated to be present in any of the 48 cases of "Anomalies of Intestinal Rotation" referred to by Dott, it was concluded that while theoretically such herniae could be accounted for in this way, the explanation demanded an unnecessarily complicated sequence of events. It was pointed out that the view held by most observers that the sacs developed from pre-existing peritoneal fossae

was probably the correct one, but even then an explanation of the formation of these herniae was required, because the pressure within the fossa is not less than the general intra-abdominal pressure. It was suggested that undue localised irritability of the intestine leading to excessive peristalsis, and the presence of a large fossa of Landzert or Waldeyer were factors of importance in determining their occurrence. Any symptoms produced by the herniae in the three cases reported were masked by the presence of some gross pathological lesion within the abdomen, but a review of the literature indicated that the majority of retroperitoneal herniae were symptomless unless acute or chronic strangulation of the intestine developed. Less frequently they gave rise to indigestion or palpable tumour formation. The interest of being able to diagnose duodenal hernia before operation by X-ray examination was commented on.

Professor G. L. Streeter demonstrated the "Lewis Gregory Film," showing the early stages of segmentation of the living rabbit egg.

Professor T. Wingate Todd gave a film demonstration of the motility of the human alimentary tract on which he made the following remarks.

It is important to realise the profound influence of subconscious emotion upon the physical characters of the alimentary tract. A study of form, position or activity of any part of the tract, not experimentally controlled for the elimination, or at least the reduction of psychic influences, is simply without any real value. These influences are indeed responsible in part for the individual variation so much emphasised to-day. When they have been successfully eliminated, the stomach and bowel respond in constant fashion whenever a particular stimulus is applied. To obtain this standard behaviour pattern for any particular individual requires practice and training. We find that it is not until the student is in his second year of medical study that his alimentary responses are likely to be constant to repetition of a stimulus, although he may have repeatedly experienced Roentgenographic examination. We find that large size (hypotony) of the stomach and absence of peristalsis in the large bowel are both induced by the fear complex, whereas increased tone with or without increased peristaltic activity is brought about by anxiety.

After elimination of emotional factors we have shown to our satisfaction that the stomach responds differently to milk and to buttermilk at 70° F. It also responds differently to milk at 150°, 70°, 30° F. and, further, the response characteristic of temperature is even more pronounced if the heat or cold is applied to the abdominal wall and this is followed by exhibition of milk at 70° F.

We find that, for a standard sized meal of constant temperature, buttermilk induces a larger stomach shadow and a peristaltic activity of greater amplitude and somewhat more rapid rhythm, compared with the behaviour pattern resulting from a milk meal in the same individual. Heat induces a very active stomach with a narrow short shadow. Cold is followed by an activity which is greatly reduced after five minutes: the stomach shadow is narrow as with heat but it differs in being long and not short.

These effects are produced reflexly and not directly, for the effects of heat and cold are greatest when applied to the abdominal wall.

Peristalsis, tone, and passage are expressions of gastric motility, and are not necessarily interdependent.

As a result of our investigations it is becoming possible to develop a standard routine technique for the analysis of stomach motility.

The investigation upon the large bowel has also progressed to a stage when its motility can be analysed. By transferring serial Roentgenograms to a cinema film we have demonstrated for the first time in practical manner the normal peristalsis of the colon. It is similar to, in many ways, but much slower than peristalsis in the stomach.

The full account of this study will be published under the joint names of Professor WINGATE TODD and Miss W. M. KUENZEL who has been associated with him in planning and carrying out the work.

A discussion on Anatomical Nomenclature was introduced by Professor T. B. JOHNSTON, and it was decided that a Committee should be elected to consider the question further and report to the Society at a subsequent date.

Mr D. STEWART and Dr S. L. WILSON read a paper on "Regional anaesthesia and the innervation of teeth."

The introduction of regional anaesthesia into dental surgery has not been as successful as might have been anticipated, on account of the fact that the teeth are often found to be sensitive after an apparently successful injection of the dental nerves. This paper contains an account of an investigation which was made to find out the cause of this residual sensibility.

On examining the condition of the pulps of teeth after a regional anaesthetic had been made, it was found that, although they were still sensitive, their reactions often differed from the conditions seen in normal cases. Frequently the only stimulus which elicited a response was the prick of a broach, while heat, cold, or pressure had apparently no effect upon them. It soon became obvious that the sensibility must be due to some other source of supply than the dental nerves. In order to trace this the areas of skin and mucous membrane rendered insensitive by the injection were marked out and recorded. In those patients in which the inferior dental nerve was anaesthetised, it was found that these areas varied to a certain extent from patient to patient. The anaesthetised area of the skin stretched from the lips above to about the lower border of the mandible below. Posteriorly this area commenced near the angle of the mouth, while anteriorly it terminated near the mid-line of the face. The areas for touch and pain did not necessarily correspond. In the mouth the area insensitive to prick was the only one which was marked out, and the area supplied by the inferior dental nerve was found to extend for a varying distance backwards from the canine. The mucous membrane behind this was supplied by the long buccal nerve, and the anterior limit of this nerve varied from the second molar to the middle of the canine.

The anaesthetised area sometimes extends across the middle line. It is difficult to assign a cause for this phenomenon, but it may be due, either to the mid-line for the nerve not corresponding to that of the body, or to the fibres for other forms of sensibility having such a different distribution to those for touch, that overlap may have been present, although it was not discovered, on account of the pain area being the only one which was examined. When the lingual nerve was anaesthetised it was found that a large area of the lingual aspect of the gum was insensitive to pain. This area occasionally only came as far forward as the canine of the same side, in other cases it reached the middle line, while in others it also crossed to the opposite side of

the body. As the long buccal nerve and the lingual were so closely associated with the innervation of the gum, it was thought that they might supply fibres to the teeth. To test this hypothesis, a number of patients, who had exposures of the pulps of the posterior teeth were given a regional injection into the inferior dental nerves, when it was found that the pulps were still sensitive. The long buccal and the lingual nerves were then injected, when it was found that the pulps were completely anaesthetised and could be removed without any inconvenience to the patients. It was necessary to inject both nerves to obtain this result. As the number of cases is small our results are only provisional; they suggest however that the supply of the pulp of the teeth is more complicated than is generally supposed, and in the case of the lower jaw comes from the lingual and the long buccal as well as from the inferior dental. These results only apply to the teeth posterior to the incisors.

Dr Tudor Jones communicated "A note on the evidence concerning the minute structure of striped muscle."

At the beginning of last year I recorded observations (*Journal of Anatomy*, vol. lxi, p. 247) which appeared to negative current hypotheses concerning the intimate structure of striped muscle. They showed that the regularly placed blocks, which, joined sideways to other similar blocks, form the "anisotropic" discs of striped muscle, are replaceable by elements distinguished from the first, since they belong to the incoming nerve rather than to the muscle. These observations were made on the muscle of the cat's ventricle and on the human ventricular muscle. Skeletal muscle exhibits differences which are only differences in arrangement and relative size of parts. The question arose whether the "muscle fibre" was not really an extraordinarily regular geometrical arrangement of interconnected nerve filaments in a bath of cytoplasm (hyaloplasm).

The structure of muscle received sustained attention from a large number of workers over a long period. But more recently the subject has been neglected possibly because it seemed that a solution could not be obtained by further discussion of available evidence.

I therefore record here some recent observations and some suggestions concerning their interpretation.

As long ago as 1891, Haycraft objected (*P.R.S.* vol. xlix, p. 287) to the "Muskelkästchen" hypothesis and the resulting osmotic theory of contraction on the ground that muscles act quickly and osmosis slowly, and on other grounds which involved the validity of the evidence available concerning the actual structure of muscle and not only the possibility or otherwise of a particular mode of action. His remarkable observations seem to have received less consideration than they merit. Haycraft showed that slight alterations of focus of the microscope could produce apparent alterations in the lights and shades of muscle comparable to similar phenomena exhibited by fine varicose glass threads, the scales of *Lepisma* or red blood corpuscles. He also called attention to the fact that so able a worker as Bowman found the "dim" and "clear" bands so undefined that he reversed the conventional order of naming them. Above all, he made impressions in drying collodion which revealed all the characteristic optical images of the muscle itself with normal illumination.

(1) These experiments were repeated with ease by me, at Winnipeg, a little more than a year ago, using Schering's celloidin shreds dissolved in a

mixture of alcohol and ether, and it then occurred to me to examine the images produced by cross-polarised light. By this means I was able to satisfy myself that the "casts," as well as the muscle, gave rise to the birefringent phenomenon: that not only muscle but the impressed surface of celloidin showed the typical "isotropic" and "anisotropic" bands. I did not know then that the physical conditions necessary for such a result had been fully elucidated. The intensity of the bands when the nicols are uncrossed is as high as with real muscle fibres; with crossed nicols it is so much reduced that some patience must be exercised if one wishes to avoid missing the images. This is to be expected because the numerous superimposed surfaces contributing to their formation in a muscle fibre are reduced to one only in the "cast." Efforts to devise means of recording these faint images photographically were unavailing. I have now been able to make permanent "casts" by the following means. Fixed and hardened muscle fibres (frog) are dehydrated completely and cleared in chloroform. A thin film of fairly thick celloidin on a glass slide is allowed to dry until a light touch with a finger nail leaves no mark visible to the naked eye. The muscle is then taken from the chloroform, blotted on filter paper, and pressed with a steel knife handle on the slide. The film with the adherent fibres is further hardened in chloroform vapour, and is then found to separate easily from the dried muscle fibres. If the appearance of striation with crossed nicols is not picked up at once, slight movements of the eye lead to their detection. The characteristic shifting of light when the stage and object are rotated in the field of polarised light is easily observed and is confirmatory of the presence of the effect which produces it. The absence of true muscle fibres has been proved by using stained fibres, staining the impressed surface and by cutting across the impressed surface with a sharp knife and attempting to stain the cut ends of muscle which might be present.

I suggest that these observations show that the images obtained by the use of cross-polarised light afford no evidence of structure beyond the fact that a series of surfaces is present. The effects produced are optical illusions of so complex a nature that the physical conditions which give rise to them cannot be determined. We have now no valid reason for believing that there is an "anisotropic substance" in muscle. The effects are akin to the patterns which manufacturers of silk and linen cloths produce by weaving. We do not commonly conclude from the familiar appearances in a table cloth that it is composed of two substances, one white and silvery and the other dull and leaden.

Haycraft's arguments were dismissed by Schäfer on the ground that staining the muscle disproved that the filials were homogeneous. I am unable to confirm this statement. Thin sections of vertebrate muscle stained by Bielschowsky's method give clearer pictures of the structure visible after fixation than even iron haematoxylin. Both these methods show great irregularity in the thickness of the stained parts but no interruption of their continuity.

(2) Evidence in favour of the theories which Haycraft criticised has been adduced from the appearances presented by so-called "contraction bands." These bands—really fusiform swellings of the muscle fibres—are supposed to represent a "wave" of "contraction" passing along the muscle fibre which has been "snapped," as it were, by a poisonous fixative reagent in the same sort of way that an express train in motion is "snapped" by a camera. The

fixative kills the organism and all its tissues, and puts an end to their physiological activity. And yet it is supposed that the intervention of death, which suspends the physiological activity of muscular contraction, does not abolish the resulting physical phenomena. This remarkable claim appears to have passed undisputed. It is, however, a very simple matter to produce such "contraction bands" at will in living vertebrate fibres, by scratching them with a needle, by over-stretching them or by damaging their surface in other ways. They are situations of injury in many ways strikingly similar to the "contraction bands" which appear when a worm is wounded by a hook. Indeed, muscle fibres do not contract by an axial longitudinal shortening. If a frog's muscle (preferably vitally-stained with methylene blue) is stimulated through its nerve electrically, a view of its contractions may be had through a microscope. Some of the fibres will then be seen to be inactive. They remain relatively straight in spite of violent movements in their neighbourhood. These movements, when active, are too rapid for study; but when active movement ceases the fibres can be seen to return to the passive state. This return is a process of straightening from a waved or spiral form, which has preceded it. The less the artificial tension in the muscle, the more waved the form of the relaxing muscle. Clear indications of this waved form are visible on strengthening the stimulus. The fibres "wriggle." Thus their ends are brought nearer to one another in the same way as the end of a whip lash is brought nearer to the handle on shaking it. These observations do not invalidate all conclusions drawn from the appearance of dead muscle. Dead fibres may be under high or low tension according to the position of the bony parts during fixation, and may show signs of the tension to which they have been subjected.

It seems, in consequence of these observations, that the only structure of muscle of which we have any knowledge is that revealed by methylene blue at some stages of vital staining and by iron haematoxylin, etc. As these are identical, I do not think they can be due to fixation, or even partial fixation. This structure is a three-dimensional network with swellings at the points of intersection of the constituent strands.

I suggest that this simple structure is amply sufficient for the production of the phenomena of contraction, more particularly so, as we have no longer to explain an axial shortening but a deformation of the fibres propagated throughout their extent.

There is therefore neither a contractile *substance* nor a receptive *substance* in muscle. There is a reticulum which in the neighbourhood of the "end-plate," is irregular and relatively accessible to the action of certain drugs (the periterminal network of Bocke). Beyond the end-plate this network presents an almost perfect regularity of arrangement, with alternating large and small nodes (at Hensen's and Krause's lines) relatively inaccessible to the action of drugs. I cannot conceive this reticulum itself being contractile and it seems absurd to attribute contractility to the cytoplasm in which it lies. But between the two there is a deformable *surface* of so minute a nature as to afford the greatest play for changes of tension both violent and sudden. It is the muscle as a whole that "contracts," not necessarily a metaphysical "substance" inside it.

Mr H. A. Harris read papers on:

(1) "The closure of the cranial sutures in relation to the evolution of the cortex cerebri."

A series of charts were exhibited to show the areas of the cerebral cortex which have been delineated by various workers from different points of approach. The main charts were:

(i) The four areas, posterior temporal, parietal, prefrontal and inferior temporal, the gradual emergence of which has been described by Elliot Smith for Pithecanthropus, Eoanthropus, Homo Rhodesiensis and other varieties of primitive man.

(ii) The prefrontal, temporal and parietal areas which have been described for primates and man, from the point of view of comparative anatomy.

(iii) The four areas described by Sir Henry Head for verbal, nominative, syntactic and semantic aphasia.

(iv) The areas of late myelinisation described by Flechsig in the prefrontal, parietal and temporal lobes.

(v) The areas of late cytoarchitectonic differentiation described by Brodmann, Campbell and Elliot Smith.

(vi) The chart showing the ages at which complete closure of the sutures of the skull occurs, based largely on the work of Wingate Todd and Lyon.

By comparison of these charts it is seen that the squamous and other circum-meatal sutures, union of which is delayed in man to extreme old age, are topographically related to the areas of the cortex above described.

The order of union of the sutures in the primates has been observed and particular attention was drawn to the skull and brain of Cebus, a typical New World monkey, in which union of the squamous suture occurs early and union of the coronal suture late. This is in accord with the small development of the temporal and parietal lobes, and the large development of the motor area. Similarly in the gorilla, the first suture to unite is the lambdoid, and it is suggested that this is related to the relatively small size of the occipital lobe. In man the lambdoid suture closes later than the sagittal, and this closure is most delayed in the area of the asterion, in relation to the highly developed posterior part of the temporal lobe.

Further observations are being pursued in primates and in congenital deaf mutes.

(2) "A preliminary note on the relation of skeletal ossification in the hind limb to the index of cerebral value of Anthony and Coupin."

The various formulae for expressing brain weight in terms of body weight were surveyed. The index of cerebral value introduced by Anthony and Coupin has been applied to a series of foetal pigs, sheep, lions and post-natal kittens of known brain weight and known body weight. Radiograms were taken and the ossification of the hind limb recorded. In each case it is found that the index of cerebral value for a given foetus bears a close relation to the index of a human presenting the same pattern and extent of ossification in the hind limb. A foetal pig of 400 gm. has an index of 0·63. The centre for the lower end of the femur is present. This centre appears in man at birth, when the index is 0·60. Similarly the pig at birth, weighing 825 gm., has an index of 1·24. The os calcis presents a secondary centre for the epiphysis. This secondary centre appears in man in the seventh year when the index is 1·21.

An attempt has been made to relate the times of ossification of the os calcis, and semicircular canals to the time of active development of the muscular system, and to the time of myelinisation of the vestibulo spinal tract. These may be related to the subjective symptoms of "quickening" in the mother.

Donaldson's conception of the rate of living in the rat as thirty times that of man has been applied to certain characters, and whilst the conception holds for many skeletal and nervous characters, it is shown to be untrue for the time of eruption of the first molar and for the time of onset of puberty, both of which are markedly delayed in man.

Various psychological deductions are tentatively outlined as a result of this demonstration of the close parallel between the development of brain mass and the development of the ossification pattern in the hind limb.

Mr Robert D. Lockhart read a paper on "Variations coincident with congenital absence of the zygoma," which will be submitted for publication in the *Journal of Anatomy*.

The skull exhibited shows absence of the zygomatic bones; a stout process half an inch long and high represents the malar, the form of which is represented as part of the superior maxilla.

The floor of the orbit slopes obliquely downwards and forwards. The condyle of the mandible is small, round and flat, the coronoid and gonion are markedly everted.

The temporalis and masseter muscles are fused. The auditory ossicles are absent save for a deformed malleus on the left side. The tympanic membrane is present on the left side. The tensor tympani muscle is well developed on both sides. The internal ear is well formed, even large.

Mr A. J. E. Cave demonstrated "Two cases of congenitally enlarged parietal foramina."

Examples of congenitally enlarged parietal foramina are somewhat rare, judging by the small number of cases recorded in the literature on the subject, although our anatomical museums must contain additional specimens. Up to 1919, R. Pamperl (*Deutsche Zeitschr. f. Chir.* Leipzig, 1919, vol. cxlviii, p. 91) could list only thirty-six recorded cases; one other case had been recorded by D. M. Greig (*Edin. Med. Journ.* 1917, vol. xviii, p. 205) in 1917; and in 1927 the same author described three further cases—two from the Museum of the Royal College of Surgeons of Edinburgh and one from the Edinburgh University Collection (D. M. Greig, *Edin. Med. Journ.* Nov. 1927) thus bringing the number of published cases up to forty.

Recently E. P. Stibbe demonstrated another example to this Society (*Proc. Anat. Soc.* 1927–28) and the present two specimens may be added to the list.

It is difficult to define the normal size of the parietal foramen, and to say when a given foramen exceeds the limits of normality, but happily, no mathematical criterion is necessary in cases of congenital enlargement of the foramen, the specimen being self-explanatory. Further, genuine cases cannot be confused with perforations of the cranial vault due to tumours, meningocele, or the pressure of Pacchionian bodies; they are simply exaggerations of the normal foramen, although the primary cause of the enlargement is still uncertain.

Lancisi (*De subitaneis mortibus*, Rome, 1707, p. 178) gave the first written

account of this condition, his case being a unilateral enlargement on the right side, the left parietal foramen being absent. Similar unilateral examples have since been recorded by Humphry, Le Double, Maggi and Gruber, although the majority of cases are those of bilateral enlargement.

Whether the condition be bilateral or unilateral depends upon the number of parietal foramina present; when one foramen is unduly enlarged, that is the only foramen present. It must be remembered that the normal foramen is subject to considerable variation as to number and position as exemplified in the following table:

Observer	Skulls	Both present	Both absent	1 foramen only	1 sagittal foramen
Greig	670	45 %	30 %	24 %	c. 3 %
Cave	100 (Ancient Egyptian)	30 %	29 %	26 %	11 %
Cave	150 (Modern)	32 %	30 %	22 %	7 %

The enlarged condition of the parietal foramen has occurred in both sexes, at all ages, is not confined to any one race or nationality and has been recognised in the living subject by radiography.

Its nature, like that of the normal foramen, is undoubtedly vascular, but some other factor must also come into force, since other vascular foramina (e.g. the mastoid), though they may be very large, never attain to the dimensions of these enlarged parietal holes. In the present instances, it would appear that a rich anastomosis through the parietal foramina, between intra- and extra-cranial vessels was the immediate cause of the enlargement, although it is obvious that a leash of vessels alone cannot have filled up the gap in the skull vault.

If, as in Turner's classical case, each foramen was occupied by a cribriform sheet of fibrous tissue, pierced by many small vessels, we are at a loss to explain why ossification failed to extend into such fibrous tissue; also, whether the presence of an abnormally large bunch of emissary veins has interfered with the local ossification. In this connection it may be noted that, in normal crania, that portion of the sagittal suture lying between the parietal foramina is always the least sinuous segment of the suture, suggesting that the parietal blood vessels partly impede the medial spread of ossification from the region of the parietal eminence.

Case A.

Thick-walled calvarium of male, aet. 74 (Leeds Anat. Dept.): sutures persistent, save posterior third of the sagittal. Bilateral, equal enlargement of the parietal foramen, each foramen lying at bottom of a "crater" (caused by bevelling of the outer table) and possessing a crenated margin.

Left foramen: roughly circular, with diameter of 5 mm.

Right foramen: 7·5 mm. horizontally × 5 mm. vertically.

On either side faint vascular grooves lead up from the back part of the temporal fossa to the parietal foramen, notching its margin; internally, numerous grooves for the posterior branches of the middle meningeal vessels stream upwards towards each foramen, there being every evidence of a rich anastomosis, during life, between the meningeal and scalp vessels. Both internally and externally faint grooves—presumably of venous origin—connect the foramina across the middle line.

Case B.

Calvarium of male, aet. 48 (Leeds Anat. Dept.). Coronal suture persistent for most part; lambdoid and sagittal sutures obliterated. Both parietal foramina enormously enlarged, circular in outline, each lying in a "crater," and the two connected by a horizontal groove both internally and externally.

Left foramen: 15 mm. diam. (admits index finger).

Right foramen: 20 mm. diam. (admits the thumb).

Bilaterally, a well-marked vascular groove ascends from the hinder part of the temporal fossa to the margin of the foramen, which it notches; on the right, an additional vascular groove leads from the occipital region to the foramen of that side. On the internal aspect of the vault several definite meningeal grooves run upwards and backwards to each foramen; again there is the strongest suggestion of an unusually well-marked anastomosis between the intra- and extra-cranial vessels through each hole.

Such an exuberant trans-parietal anastomosis has been established by dissection in certain cases recorded in the literature on the subject.

Symmetrical thinness of parietal bones.

The specimen is the calvarium of an adult female, recently dissected in the Leeds Anatomical Department, showing congenital symmetrical thinness of the parietals, and a similar condition of each pterionic area.

In the hinder half of each parietal between the sagittal suture and the superior temporal crest, there is a definite, shallow, antero-posterior depression, the bone here being semi-translucent. The concavity on the external cranial surface is definite though not deep, and there is no corresponding convexity on the inner cranial surface. Consequently the condition is not brought about (as has been frequently suggested) by external pressure. In the thin regions the outer table, though differing somewhat in texture from that elsewhere, is quite free from pathological change and exhibits no sign of erosion or atrophy. The inner table is normally developed, is well-marked by the hindmost meningeal vessels, and, owing to the absence of the diploe in this region, lies in apposition with the outer table.

In the pterionic region of each parietal also, and extending on to the contiguous portion of the frontal bone, is a similar area of congenital thinness of the cranial vault, possessing features similar to those seen in the posterior parietal depressions. Inspection of the saw-cut reveals the cause of the thinness as a local congenital absence of the diploe—this being the true explanation of the whole condition, whether affecting the parietal bone, the pterionic region, or the planum occipitale.

Mr Robert D. Lockhart gave a demonstration of the connections of "The anterior commissure of the brain."

The form and connections of the anterior commissure in man, horse, cow, sheep, dog, cat, hare, rabbit, guinea-pig, squirrel and rat were illustrated by a series of blunt dissections.

The method affords easy and graphic demonstration of features, seldom appreciated in their real dimensions, even by serial histological sections in the three planes.

The following points were emphasised:

More particularly in the hare, but also in the rabbit, guinea-pig, squirrel and cat, there is a peculiarly rich radiation of the fibres of the temporal or

posterior portion of the commissure, over the lateral aspect of the lenticular nucleus as well as towards the occipital pole.

In the horse, cow, sheep and dog the posterior portion is much smaller.

In the sheep the posterior portion may be traced deeply into the internal capsule.

In man, the fibres of the posterior portion of the commissure may be traced to the anterior parts of the temporal gyri, but the majority of the fibres, after tunnelling the corpus striatum, lie on the postero-infero-lateral aspect of the lenticular nucleus before coursing occipitalwards along the roof of the descending horn of the lateral ventricle, superior to the optic radiation. The temporal portion is remarkably large in man but it does not have the extensive relation to the lateral surface of the lenticular nucleus seen in some animals.

The anterior portion small in man, large in animal brains, may be traced through the anterior limb of the internal capsule to the olfactory bulb and frontal region, and apparently to the corpus striatum also.

Certain problematic and controversial considerations arising out of this investigation will be more readily discussed in a future communication in conjunction with clinical and experimental evidence.

Professor J. S. B. Stopford read a paper on "The great vein of Galen," of which the following is a summary:

A demonstration of lantern slides and a dissection was presented to show the course and relations of the great vein of Galen and the significance of this vessel in the production of raised intra-cranial pressure associated with tumours within the skull.

From the dissection it was seen that the vein curves round, and is throughout its course in intimate contact with, the splenium of the corpus callosum. Thus from its origin the vein passes at first backwards and upwards, and then forwards and upwards, to reach the hinder end of the inferior longitudinal sinus, which it enters against the flow of blood within the sinus. Consequently the vein is in such a position that it must be compressed against the splenium by anything which raises the tentorium. The tentorium may be elevated directly by pressure from below, and Elsberg and Silbert[1] have proved recently that elevation is commonly caused by infratentorial tumours, or indirectly by deflection of the falx. Owing to the shape of the falx this structure is more likely to be deflected by supra-tentorial tumours in the parieto-occipital and occipital regions than those in the frontal or parietal. Post-mortem and clinical statistics from the Manchester Royal Infirmary, during the twenty-five years 1901–25, of cases of intra-cranial tumour were presented to show that signs of raised intra-cranial pressure never occurred in a third of the patients suffering from growths in the frontal and parietal regions, whereas it was almost constantly a feature in cases of parieto-occipital and occipital tumours.

It is generally agreed that the site of the tumour appears to be the important factor with regard to the occurrence or absence of signs of raised intra-cranial pressure. Situations which most frequently give rise to raised pressure are those in which compression of the great vein of Galen is most likely to be produced, and owing to the anatomical arrangement of the drainage of the choroid plexuses such compression would inevitably induce an excessive

[1] Elsberg, C. A. and Silbert, S. "Changes in size and relations of lateral ventricles in tumours of brain—a preliminary report." *Archiv. of Neurol. and Psychiat.* 1925, vol. xiv, pp. 489–501.

production of cerebro-spinal fluid and consequent rise of pressure within the cranium.

Dr A. C. KELLY exhibited dissections showing the peripheral distribution of the facial nerve.

Mr G. JEFFERSON and Mr D. STEWART showed specimens of skulls illustrating the mode of termination of frontal diploic veins in the veins accompanying the middle meningeal artery.

Professor EVATT demonstrated specimens of:

(*a*) Long bones showing two centres of ossification and two nutrient foramina.

(*b*) The development and morphology of the basement membrane.

Dr C. STARKIE and Mr D. STEWART gave a demonstration of the constituents of the inferior dental nerve plexus, an account of which will be submitted for publication in the *Journal of Anatomy*.

Miss EUGENIA R. O. COOPER demonstrated a series of histological sections, an account of which will be submitted for publication in the *Journal of Anatomy*.

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THE THALAMUS OF *TUPAIA MINOR*

By W. E. LE GROS CLARK, D.Sc.

The comparative study of the mammalian optic thalamus has reached a much less advanced stage than has that of many other parts of the brain. The homologies of the various thalamic nuclei of Mammals are far from settled and the attempt to determine them is fraught with great difficulties. This is partly due to the difficulty of defining certain elements of the thalamus unless detailed attention is paid to the cyto-architecture as well as the myelo-architecture, partly to the varied nomenclature used by different authors (which is in no way unusual in the history of the study of cerebral morphology), and partly to the very few adequate accounts of the mammalian thalamus which are available. Especially patent is the gap in our knowledge when an attempt is made to compare the thalamus of Primates with that of lower mammals, and the importance of this will be realised when consideration is given to the application of experimental work on the thalamic region of lower mammals to thalamic functions in Primates, including man. Even such a definite unit as the lateral geniculate body needs to be more carefully defined in morphological terms, for it is not at all clear that all experimental observers mean precisely the same element or group of elements when they use this term. It is very necessary, before sound progress can be made in this subject, that full descriptions of the thalamus of a number of different mammals should be available and that studies of a closely graded series of mammalian brains should be made in order to establish satisfactory homologies, for there seems to be a wide variation in the differential development of certain thalamic nuclei in different mammalian groups. It seemed likely that the brain of the tree-shrew would provide useful material for the study of the mammalian thalamus. In the first place the brain of this small insectivore is a relatively simple and generalised brain, but at the same time shows marked characteristics of its own in the reduction of the olfactory elements and a conspicuous development of the visual elements. Also *Tupaia* has for some time been regarded by many morphologists as probably a representative (not very modified) of the group of mammals from which presumably the primate phylum originated in Mesozoic times. Further, the thalamus of *Tupaia* offers itself for a fair comparison with that of other insectivores, whose brains are of comparable size but which exhibit very considerable differences in the development of the various elements of the cerebrum. Such a differential development is to a large extent reflected in the structure of the thalamus, and it seems feasible to suppose that a comparative study of this kind might yield valuable anatomical evidence concerning the significance of the different thalamic nuclei.

MATERIAL AND METHODS

The present study has been mainly based upon the examination of a series of transverse sections of the brain of *Tupaia minor*. Alternate sections, cut at 15μ, were mounted and stained with toluidin blue. A second series of transverse sections, stained alternately with toluidin blue and iron haematoxylin, was also used. The iron haematoxylin staining in the material available was not sufficiently successful to allow the finer terminations of the myelinated fibres to be traced with certainty but it provided a useful, and indeed necessary, adjunct to the study of the cyto-architecture of the thalamus in the first series. For descriptive purposes, the alternate sections of the first series have been numbered consecutively from before backwards, the most rostral section in which the anterior nucleus of the thalamus first appears being regarded as the first section. To give an idea of the extent of the thalamus in these sections it may here be noted that the anterior margin of the anterior colliculus first appears at section 121. In the descriptive account of the nuclear masses of the thalamus, references are frequently made to this section numbering in order to convey an accurate impression of position and extent in the sagittal direction. It is thought that this method of indicating planes antero-posteriorly has a distinct advantage over that which depends upon reference to the position of the variable nuclear elements of the thalamus, especially for comparative purposes.

Attempts have been made to bring the description into line with the work of previous authors on the mammalian thalamus with special reference to Cajal (2), Munzer and Wiener (19), Winkler and Potter (27), Sachs (22), Friedemann (8), Pines (21), Tsai (24), and Gurdjian (11). The latter has lately published a detailed account of the diencephalon of the albino rat which has been found of great value in the present study. As far as possible, the nomenclature used by Gurdjian has been used here and references have been made to synonyms used by previous writers.

LIST OF ABBREVIATIONS

A.C.	Anterior colliculus.	*L.M.L.*	Lamina medullaris lateralis.
A.Rsp.	Area retrosplenialis.	*L.M.V.*	Lamina medullaris ventralis.
C.C.	Corpus callosum.	*M.C.*	Meynert's commissure.
C.F.	Fornix commissure.	*M.F.*	Medial fillet.
C.G.L.	Corpus geniculatum laterale.	*M.F.B.*	Medial forebrain bundle.
C.G.M.	Corpus geniculatum mediale.	*N.A.d.*	Nucleus antero-dorsalis.
C.L.	Corpus Luysii.	*N.A.m.*	Nucleus antero-medialis.
C.M.	Corpus mammillare.	*N.A.v.*	Nucleus antero-ventralis.
C.P.	Posterior commissure.	*N.C.*	Nucleus centralis.
Ch.Op.	Optic chiasma.	*N.Cd.*	Nucleus caudatus.
D.T.V.	Ventral decussation of tegmentum.	*N.D.R.*	Nucleus dorsalis raphae.
F.	Fornix.	*N.E.*	Nucleus entopeduncularis.
F.R.	Fasciculus retroflexus.	*N.Fi.*	Nucleus filiformis.
G.C.	Gudden's commissure.	*N.H.*	Nucleus habenularis.
G.I.	Ganglion interpedunculare.	*N.Hy.A.*	Nucleus hypothalamicus anterior.
Gl.P.	Globus pallidus.	*N.Hy.L.*	Nucleus hypothalamicus lateralis.

N.Hy.M.	Nucleus hypothalamicus medialis.	*N.V.al.*	Nucleus ventralis antero-lateralis.
N.L.a.	Nucleus lateralis A.	*N.V.am.*	Nucleus ventralis antero-medialis.
N.L.b.	Nucleus lateralis B.	*N.V.pl.*	Nucleus ventralis postero-lateralis.
N.L.p.p.	Nucleus lateralis, pars posterior.		
N.M.Hy.	Nucleus magnocellularis hypothalamicus.	*N.V.pm.*	Nucleus ventralis postero-medialis.
N.Md.	Nucleus dorso-medialis.	*P.C.*	Posterior colliculus.
N.O.	Optic nerve.	*P.C.M.*	Pedunculus corpori mammillaris.
N.Oc.	Nucleus oculomotorius.	*P.P.*	Pes pedunculi.
N.Op.T.	Nucleus opticus tegmenti.	*P.Th.I.*	Inferior peduncle of thalamus.
N.Ov.	Nucleus ovoidus.	*R.T.*	Thalamic radiations.
N.P.	Nucleus posterior.	*S.Calc.*	Sulcus calcarinus.
N.Pa.	Nucleus parataenialis.	*S.N.*	Substantia nigra.
N.Pc.	Nucleus paracentralis.	*S.T.*	Stria terminalis.
N.Pf.	Nucleus parafascicularis.	*Str.M.*	Stria medullaris.
N.Pt.	Nucleus pretectalis.	*T.C.*	Tuber cinereum.
N.R.	Nucleus reticularis.	*T.O.*	Optic tract.
N.Rb.	Nucleus ruber.	*Tr.Op.Ac.P.*	Posterior accessory optic tract.
N.Re.	Nucleus reuniens.	*V.A.*	Bundle of Vicq d'Azyr.
N.Rh.	Nucleus rhomboideus.	*Z.I.*	Zona incerta.
N.T.	Nucleus tangentialis.	*III.*	Third cranial nerve.

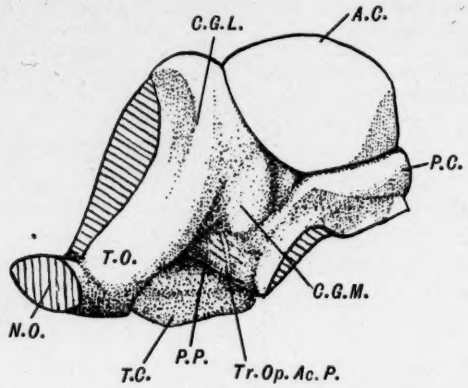
THE BRAIN OF *TUPAIA MINOR*

For an adequate appreciation of the structure of the thalamus of *Tupaia* it is essential to be acquainted with the main features of the anatomy of the brain as a whole. I have previously described the brain of this interesting animal in a general way, with special reference to cortical structure (3). The olfactory bulbs, tuberculum olfactorium, piriform lobe and hippocampal formation are all somewhat reduced when comparison is made with the brains of other insectivores. The neopallium is well differentiated and produced caudally and ventrally into definite occipital and temporal poles. The calcarine sulcus is visible macroscopically, while microscopically indications of the intercalary and suprasylvian sulci may be demonstrated. In the larger tree-shrews (e.g. *Tupaia ferruginea*) these sulci are much more evident. One of the most pronounced characteristics of the neopallium is the extent and differentiation of the *area striata* which, on the medial surface of the hemisphere, extends forwards and downwards as far as the dorsal surface of the corpus callosum. The corpus callosum is well developed, while the anterior commissure is small. The optic nerves, chiasma, and tracts are conspicuously large, the latter (text-fig. 1) measuring about 2 mm. in width. The lateral geniculate body lies under cover of the optic tract as it sweeps up the side of the thalamus, but the limits of the body are not visible from the surface[1]. Immediately posterior to the lower pole of the lateral geniculate body is an oval eminence which projects on the surface and which is the medial geniculate body. The anterior colliculus is relatively huge and recalls in its appearance the optic lobe of a reptilian brain. The posterior colliculus, on the contrary, is very

[1] In my paper "On the brain of the Tree-shrew" (*P.Z.S.* 1924), the medial geniculate body has been erroneously labelled "lateral geniculate body" in fig. 14.

inconspicuous, forming a strip which lies under cover of the posterior border of the anterior colliculus and again recalling a reptilian condition. Crossing over the crus cerebri to reach its medial aspect can be seen the fine posterior accessory optic tract (tractus peduncularis transversus).

In general, then, the brain of *Tupaia* is somewhat large and well developed in comparison with the brains of other insectivores. It exhibits a relative diminution of the olfactory regions, a definite hypoplasia of the secondary auditory centres (correlated with an atrophy of the external ear), and a very



Text-fig. 1. Lateral view of thalamus and mid-brain of *Tupaia minor*. (×6.)

marked development of those parts of the brain which are mainly concerned with the reception and interpretation of visual impulses. The characteristic features of the tree-shrew's brain may be directly the resultant of the arboreal habits of the animal, but they are also such as have been postulated for the brain of the ancestral form from which the Primates have presumably been derived. If the details of the brain are considered in conjunction with many other features of the general anatomy of *Tupaia*, the possibility, at least, must be conceded that the tree-shrews have a real phylogenetic relationship with the primate phylum. In any case, there can hardly be any doubt that *Tupaia* is a very generalised eutherian mammal which shows a striking combination of primitive and progressive morphological characters.

THE NUCLEAR ELEMENTS OF THE THALAMUS

Nucleus Anterior. (Pl. I, figs. 2, 3, *N.A.d.*, *N.A.v.*, *N.A.m.*)

The anterior nucleus of the thalamus is readily identified by its position and relation to fibre systems, by its well-defined form, and by the features of its component cells. It may be clearly divided into a main or principal nucleus and a smaller dorsal nucleus. The principal nucleus begins at section 1 as an

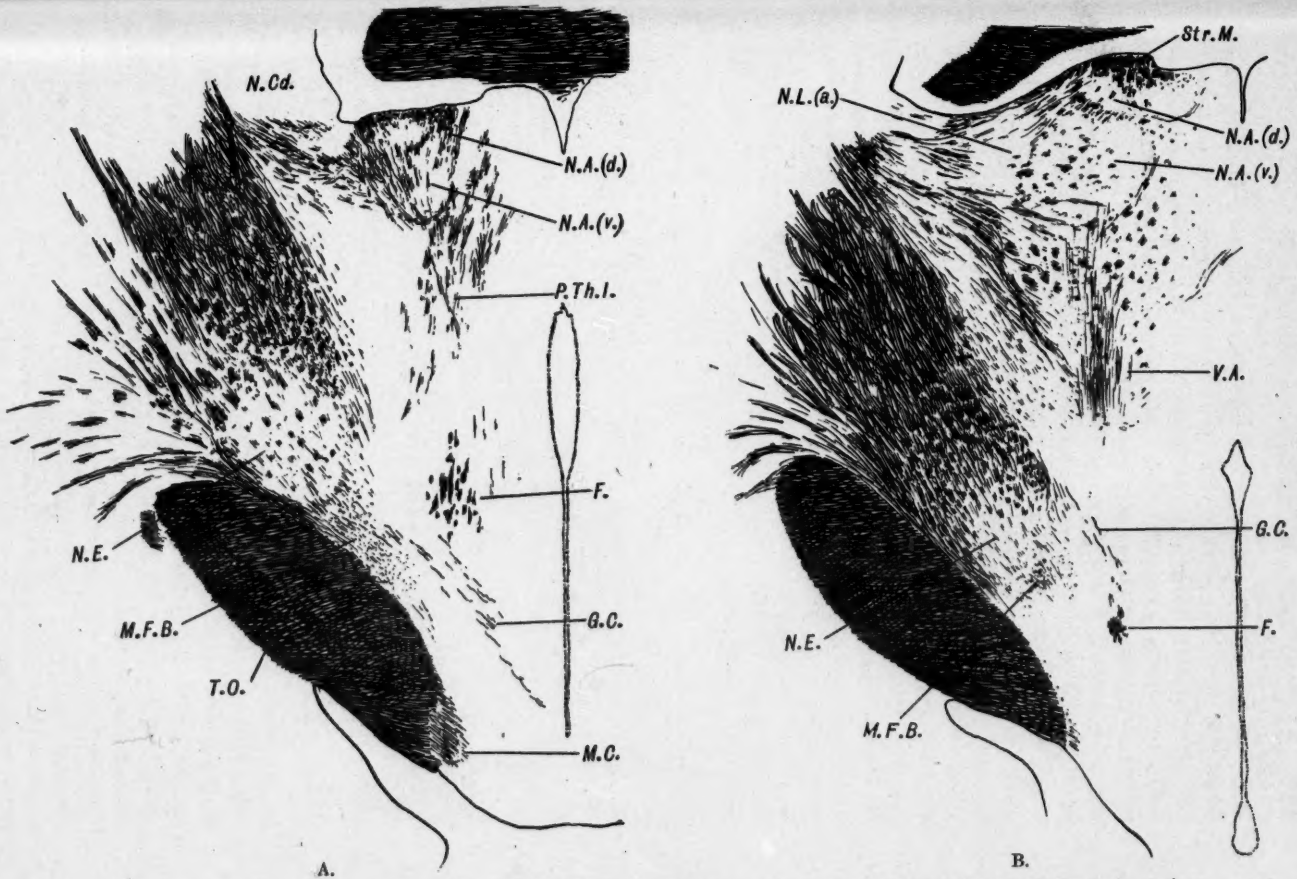
oval group of rather small cells vertically disposed close to the dorsal surface of the thalamus between the descending fibres of the stria terminalis laterally and the rhinencephalo-habenularis component of the pedunculus inferior thalami medially. A few sections more caudally it takes on a more characteristic appearance, forming a circumscribed circular group of medium, rounded or oval cells between the parataenial nucleus and the nucleus reticularis. Almost at once, it begins to extend medio-ventrally, ventral to the parataenial nucleus, towards the mid-line. This medio-ventral extension in some sections is distinctly separated from the lateral portion of the main nucleus by a cell-free zone, and this separation becomes much more evident caudally. These two parts, lateral and medial, clearly correspond to the nucleus anterior ventralis and nucleus anterior medialis of Munzer and Wiener, Gurdjian, etc. They are, however, composed of precisely the same type of cell and in many sections are not to be distinguished on the basis of cyto-architecture. The distinction between them is more evident in myelin-stained sections. At section 12 the medial extremity of the antero-medial nucleus comes up against the mid-line where it abuts upon the small raphe cells which here correspond to the nucleus dorsalis raphae, but separated from them by a medullary lamina. At section 25 the antero-medial nucleus becomes less distinct and its cells more scattered, and at section 30 it appears to be connected with its fellow of the opposite side by an irregular bridge of cells of the same type as those of the nucleus itself, but rather smaller (Cajal's interdorsal nucleus). More caudally the medial extremity of the nucleus can only be distinguished with difficulty as a few scattered cells lying close to the mid-line, in some sections apparently connected across the mid-line by raphe cells, and finally disappearing at section 45. The antero-lateral nucleus is better defined. The cells in the ventral part tend to be rather smaller than in the rest of the nucleus and, at section 26, this smaller-celled element is marked off from the rest of the nucleus by a comparatively cell-free zone. These two parts of the antero-ventral nucleus appear to correspond to the nuclei *aa* and *ab* described by Pines in the lemur. The antero-ventral nucleus terminates at section 44.

The small dorsal element of the anterior nucleus corresponds to the nucleus antero-dorsalis of many authors and to Monakow's n. anterior C, to Winkler's n. anterior B, and Cajal's noyau angulaire. It can be distinguished from the main nucleus by its more deeply staining cells and by their close formation. It forms a cap on the top of the main nucleus and is separated from it by a well-defined clear band. It appears rostrally at section 12 as a group of small fusiform cells disposed with their axes transverse, and fairly densely packed together. Caudally it enlarges slightly, the cells becoming more polygonal and more irregularly arranged. The constituent cells in general are not larger than the typical cell of the main anterior nucleus and many of them are much smaller. In section 25 the two antero-dorsal nuclei are connected across the mid-line by a band of medium and small cells representing the bed nucleus of the commissure linking up the two nuclei (n. commissuralis inter-antero-

dorsalis). The antero-dorsal nucleus disappears posteriorly a few sections before the disappearance of the main anterior nucleus. Fibres of the superior thalamic radiation can be seen in the iron haematoxylin sections penetrating into the n. antero-ventralis and n. antero-dorsalis, and passing laterally to form a dense layer immediately ventral to the nucleus caudatus (stratum subcaudatum of Sachs). According to the experimental observations of Sachs (23), these fibres do not extend laterally beyond the caudate nucleus, and they are thus to be regarded as thalamo-striatal in nature. Huber and Crossby, in their work on the brain of the alligator (14), corroborate this. Fibres of the superior thalamic radiation could not be followed into the antero-medial nucleus, and herein we find agreement with the observations of Gurdjian. The fibres of the tractus mammillo-thalamicus appear to terminate largely in relation with the ventral aspect of the antero-ventral nucleus, though some seem to be related to the antero-medial nucleus also. None could be traced into the substance of the antero-dorsal nucleus. It may be noted that Gurdjian, in the brain of the rat (11), concludes that the bundle of Vicq d'Azyr is more intimately associated with the antero-medial than with the antero-ventral nucleus. Our observations are more in accord with the figures of this part of the thalamus in the rabbit's brain as shown by Winkler and Potter. Sachs also found, experimentally, that some fibres run back from the anterior nucleus to break up in the outer part of his median nucleus.

The identification of the antero-dorsal and antero-ventral nuclei offers no difficulty. As regards the antero-medial nucleus, this quite clearly corresponds to Gurdjian's nucleus of the same name in the rat. It is not specified in Pines' work on the lemur (21), but it apparently corresponds to the medio-central extension of his nucleus *aa* (fig. 12), and more caudally to a mass of cells (shown in his excellent photographs but not labelled) lying close to the midline between his n. parataenialis and n. submedialis. It seems that Monakow and Winkler include this nucleus in their group of medial nuclei, and Winkler's nucleus Mb (27) perhaps represents it. On the basis of myelo-architecture it appears to be so distinct from the antero-ventral nucleus that it might be considered inadvisable to associate the two nuclei. But the cell type is similar, and, as noted above, Gurdjian states that in the rat the greater part of the bundle of Vicq d'Azyr ends in relation to the antero-medial nucleus.

Comparatively, the elements of the anterior nucleus in *Tupaia* are developed to an extent similar to that in the rabbit. The antero-dorsal and antero-medial elements (especially the former) are not so extensive as they are in the rat (as represented by Gurdjian). This comparison is the more instructive since, in size and general form, the cerebrum of the rat resembles that of *Tupaia*. In comparison with *Lemur*, the antero-dorsal and antero-medial nuclei appear rather larger. A feature of the antero-dorsal nucleus which calls for note is the size of its constituent cells. These do not surpass in this character those of the antero-ventral nucleus, although they are more darkly stained. Indeed, many of them are much smaller. Cajal, in describing the cells of this nucleus



Text-fig. 2. Transverse sections through the thalamus of *Tupaia minor* (second series, iron haematoxylin). A. At level of anterior end of thalamus. B. At level of termination of the mammillo-thalamic bundle.

in the mouse, remarks on "leur volume, très supérieur à celui de tous les autres corpuscles de la couche optique," and this is a feature to be found in most lower mammals. In Primates, however, the component cells are not distinguished for their size (Pines, Friedemann). It should be noted that Brunner and Spiegel(1), in their paper on the brain of the marmoset, and, following them, Woollard(29), in his account of the epithalamus of *Tarsius*, call this nucleus the nucleus disseminatus, a name applied by other authors (e.g. Pines) to diffuse groups of small cells situated on the dorsal aspect of the thalamus more posteriorly[1]. In a primitive mammal like *Macroscelides*, the cells of the antero-dorsal nucleus reach an astonishing size, perhaps associated in this animal with the inordinate development of the hippocampus. It appears, then, that the relatively inconspicuous size of the cells of this nucleus in *Tupaia* may be regarded as a progressive feature, probably correlated with the diminution of the olfactory regions of the brain. It will also be realised, from this account, that it is not always possible to homologise nuclear masses of the thalamus by reference to the characters of the constituent cells.

According to Cajal, the antero-dorsal nucleus probably receives afferents from the bundle of Vicq d'Azyr, the fibres having previously passed through the antero-ventral nucleus.

Nucleus Habenulae. (Pl. II, figs. 4, 5, *N.H.*)

This nucleus first appears at section 61 as a flattened band of deeply staining medium-sized cells, closely packed together, lying immediately under the ependyma at the dorso-medial border of the thalamus. It increases progressively but slowly in size as far caudally as section 121 (where the habenular commissure appears), after which it diminishes in size until it disappears at section 129. Lateral to the habenular ganglion are to be seen scattered groups of small cells on the dorsal surface of the thalamus, which probably correspond to the pars lateralis of the habenular nucleus described by Tsai in the opossum. In text-fig. 3 A can be seen the commencement of Meynert's bundle, formed by the two limbs, lateral and medial, which arise from corresponding parts of the habenular nucleus.

Nucleus Parataenialis. (Pl. I, figs. 1–3, *N.Pa.*)

This nucleus appears in the first section as a small collection of medium cells scattered irregularly at the dorso-medial border of the thalamus immediately medial to the stria medullaris. Caudally, it at first shows a tendency to extend in a ventral direction and to run into the collection of cells found

[1] Obersteiner first(20) applied the name "nuclei disseminati" to very variable small oval nuclei found (but not always) on the dorsal surface of the thalamus of the human brain. It is not clear whether these nuclei are to be regarded as the remnants of the antero-dorsal nucleus in man, but Sachs later applied the term to the antero-dorsal nucleus of mammals generally, though from his descriptions it is not clear whether he confines the term to this particular cell group. It would be better at present for the sake of clarity to reserve the name "nucleus disseminatus" for use in the sense implied by Obersteiner.

at this level on either side of the dorsal extremity of the median raphe. Soon, however, these cells collect into a fairly dense mass dorsally. By section 10, two parts of the parataenial nucleus can be recognised, a medial part consisting of small cells and a lateral part with medium-sized cells. The latter element comes to lie up against the antero-ventral nucleus, but separated from it by a cell-free zone. At first the two parts are not sharply delimited, but by section 30 the distinction is clear, for they are here separated by a clear band. In many sections the cells of the medial group pass uninterruptedly into the cells of the dorsal end of the median raphe, here forming the nucleus dorsalis raphae. The lateral large-celled part diminishes to a few scattered cells at section 44, and the medial small-celled element also becomes very small at this level. By section 52, the lateral element is no longer recognisable and becomes replaced behind this point by a small irregular band of fusiform cells with horizontal axes, lying transversely above the dorso-medial nucleus. These small collections of cells correspond to the nuclei disseminati of other authors.

Nucleus Reticularis. (Pls. I, II, figs. 1–4, *N.R.*)

There is no need to describe this nucleus in detail, for its features are identical with those found in mammals generally. As far caudally as the plane where the ventral nucleus becomes prominent, the nucleus reticularis forms a conspicuous mass of medium and large angular cells, well stained with toluidin blue, scattered among the fibres of the thalamic radiations. Rostrally it appears as a few cells extending ventrally lateral to the descending fibres of the stria terminalis. It quickly broadens out and comes to lie on the lateral aspect of the antero-ventral nucleus. From this it becomes separated by the pars anterior of the lateral nucleus, and its dorsal extremity becomes pushed down on the lateral aspect of the thalamus by the appearance above of the principal part of the lateral nucleus and by the corpus geniculatum laterale. Ventrally, it bounds the ventral nucleus laterally and below and eventually becomes compressed into a narrow band of cells extending into the zona incerta between the ventral nucleus and the pes pedunculi. Gurdjian has emphasised the intimate relation between this nucleus and the thalamic radiations.

Entopeduncular Nucleus. (Pl. I, fig. 2, text-figs. 2 A, B, *N.E.*)

This nucleus is well developed in *Tupaia* and, by reason of its position at the inner end of the pes pedunculi, is more conspicuous in myelin-stained sections. It first appears at section 12, lying here just above the lateral margin of the optic chiasma, between the ventro-medial end of the globus pallidus and the lateral hypothalamic area, being separated from these two regions by cell-free gaps and bounded medially by the lower end of the inferior peduncle of the thalamus. The nucleus consists of cells which are scattered, generally triangular and rather elongated in shape, and a little smaller than those which form the globus pallidus. At section 27 it becomes well developed, here forming a spherical circumscribed group of cells embedded in the lower end of the lateral

forebrain bundle. More caudally it diminishes until, by section 50, it has disappeared altogether. Gurdjian regards this nucleus as a "substation for descending impulses through a group of peduncular fibres."

The entopeduncular nucleus has been described by Huber and Crossby in the alligator, by de Lange in *Testudo*, and by Edinger in *Varanus*.

Nucleus Lateralis.

Under this heading are grouped together, mainly for gross topographical and comparative reasons, a number of nuclear masses which occupy the dorso-lateral region of the thalamus.

Anteriorly is a fairly well-defined nucleus which may here be called *nucleus lateralis A* (text-fig. 2 B). It is composed of cells which closely resemble those of the pars posterior of the lateral nucleus (*vide infra*) except that they are rather more rounded. It is clearly separated from surrounding nuclei by medullary bands and it is penetrated by bundles of fibres derived from the superior thalamic radiations which tend to give a laminated appearance to its cells. It appears rostrally at section 25, lateral to the antero-dorsal nucleus, bounded ventro-laterally by the upper end of the reticular nucleus and ventro-medially by the antero-ventral nucleus. It reaches its maximum size in transverse section at section 40, where it raises up the upper and outer angle of the thalamus into a small eminence covered above by the fimbria. Further back it shrinks rapidly and comes into relation with the lateral extremity of the paracentral nucleus. It then becomes sandwiched in between the anterior end of the pars posterior of the lateral nucleus and the habenular nucleus and displaced ventrally. Here it is very poorly defined and seems to run into the rostral end of *nucleus lateralis B*. The latter element (Pl. I, fig. 3, *N.L.b.*) is a collection of cells which appears at the tip of the dorso-lateral extremity of the antero-lateral ventral nucleus, at first distinct from the latter, but caudally merging with it. It shows itself at section 58 as a distinct group of cells immediately below the anterior extremity of the pars posterior of the lateral nucleus in the position occupied more rostrally by the ventral extremity of the nucleus lateralis A. It is composed of cells of medium and small size somewhat irregularly arranged, but it may be noted that the peripheral cells of the group are rather smaller and there is a central core of larger deeply staining angular cells closely packed together. It is linked up with the lateral extremity of the paracentral nucleus which, with the central nucleus, appears to form a bed commissure connecting it with the corresponding nucleus of the opposite side. Traced caudally, the nucleus becomes less distinctly defined and the central core less conspicuous. At section 70 it is in relation with the lateral geniculate body laterally, separated by the lateral medullary lamina, with the pars posterior of the lateral nucleus dorsally (also separated by a medullary lamina), and ventrally with the antero-lateral ventral nucleus, with which it is directly connected by a collection of small cells. Further caudally, at section 80, it loses its identity and runs without interrup-

tion into the upturned dorso-lateral extremity of the antero-lateral ventral nucleus. Its union with the latter might seem to justify its inclusion in the group of ventral thalamic nuclei in spite of its dorsal position anteriorly. But for topographical reasons, and because it seems to correspond with an element of the lateral nucleus described by other authors, it is here included in the group of lateral nuclei. It may also be noted that a clear distinction between ventral and lateral nuclei in the thalamus has been found difficult or impossible to demonstrate by previous writers. The B element here described would appear to correspond to the anterior extremity of Cajal's "noyau sensitif," which (as this author notes in the case of rodents) narrows anteriorly and in this direction reaches up to the reticular nucleus and the antero-ventral nucleus. Munzer and Wiener (19) describe in the rabbit a nucleus which occupies a corresponding position (but apparently more extensive) which they call the nucleus magnocellularis, and its constituent cells, which are described as "auffallend grossen, dunkelblau tingierten Zellen," seem to resemble in character those found in the centre of nucleus lateralis B.

By far the greater part of the lateral nucleus is made up of an element which quite clearly corresponds to the pars posterior of the lateral nucleus which has been described by Gurdjian in the rat's brain, but which in the latter animal is relatively small and insignificant. He describes this element as being continuous anteriorly with the main lateral nucleus (which corresponds to element A in *Tupaia*) and as being formed of cells of the same type. He further states that it is distinguished by receiving optic fibres and by having a special cortical connection through the superior thalamic radiation. In *Tupaia* the pars posterior is very closely associated with the visual elements of the thalamus. Thus it is covered on its free surface everywhere by the optic tract, some of whose fibres penetrate into it. It is not possible from these preparations to say whether these optic-tract fibres terminate in part in the nucleus (as they do in the rat according to Gurdjian) or whether they all pass through the nucleus to reach the tectum and pretectal nucleus. In some sections, these penetrating fibres give to the cells of the pars posterior a feeble lamination. The pars posterior of the lateral nucleus becomes sandwiched in between the lateral geniculate body and the pretectal nucleus, and with these nuclei appears to form an anatomical system very distinctly cut off from the rest of the thalamus by the pronounced lateral medullary lamina.

The pars posterior of the lateral nucleus (Pls. I–III, figs. 3–7, text-figs. 3 A, B, *N.L.p.p.*) first shows itself at section 54, where the upper end of the optic tract also appears rostrally. It is here bounded laterally by the anterior extremity of the dorsal nucleus of the lateral geniculate body, medially by the dorso-medial nucleus and the parataenial nucleus and separated from the latter on the upper surface of the thalamus by a small superficial blood vessel, ventrally by the element B of the lateral nucleus. It is everywhere marked off from neighbouring nuclear groups (with the exception of the lateral geniculate body) by a very clear medullary lamina. Its cells (which

closely resemble those of the nucleus lateralis A) are of medium size, mainly triangular or fusiform in shape, uniformly but rather lightly stained, and sparsely but regularly distributed. The more superficial cells tend, somewhat obscurely, to be arranged in rows which run parallel to the optic-tract fibres which cover them. Traced caudally, the ventral margin of the nucleus extends ventrally down the lateral margin of the thalamus as the lateral geniculate body descends. At section 109 (Pl. II, fig. 5) the nucleus pretectalis begins to separate it from the habenular nucleus above. In this transverse plane the pars posterior of the lateral nucleus is triangular in section, its lower angle reaching down to the mid-point of the medial margin of the dorsal nucleus of the lateral geniculate body. Here, also, it reaches its maximum size in cross-section. Further back, it becomes compressed by the rapidly growing pretectal nucleus, and at section 154, where the lateral geniculate body comes to an end, it forms a small triangular nucleus lying between the pretectal nucleus above and the medial geniculate body below. Eventually it fades away at section 162. In the whole of its antero-posterior extent, the pars posterior of the lateral nucleus is covered superficially by the optic tract.

The close relation between the pars posterior of the lateral nucleus and the lateral geniculate body and the overlying optic tract, and the penetration of the nucleus by optic-tract fibres, some of which probably terminate therein (apart from the question as to whether these may be retinal fibres or not), suggest that the nucleus has some association with visual functions. Moreover, in *Tupaia*, in which the visual elements of the forebrain are highly differentiated, the pars posterior of the lateral nucleus is conspicuously large, and it is mainly responsible for the displacement of the dorsal nucleus of the lateral geniculate body to the ventral position which it occupies caudally. A comparison with the thalamus of an insectivore like *Macroscelides*, which is approximately of the same size as *Tupaia* and in which, although the optic nerves and the anterior colliculi are very large, the lateral geniculate body and the cortical representation of vision are feebly developed, is instructive, for there the pars posterior of the lateral nucleus is very insignificant. Again, judging from a text-figure given by Brunner and Spiegel (1), in *Sciurus*, in which, compared with other rodents, the optic nerves are large and the area striata of the cortex well differentiated (Fortuyn (9)), the pars posterior of the lateral nucleus is relatively much larger than in the rat. There seems, indeed, some justification for supposing that the pars posterior of the lateral nucleus is homologous, at least in part, with the pulvinar of the primate thalamus. The relation of the pars posterior to the lateral geniculate body and the fibres of the optic tract and the characters of the constituent cells of this nucleus are similar to those of the pulvinar. Gurdjian's statement that, in the rat, the pars posterior of the lateral nucleus has "a special cortical connection through the superior thalamic radiation" is in harmony with this suggestion, for it has been demonstrated that the pulvinar of Primates has wide cortical connections, especially with the region of the angular gyrus (Minskowski). Brunner and

Spiegel give a brief description of the pulvinar in the brain of the marmoset and state that its constituent cells are of the same type as those of the lateral nucleus and that it has no sharp boundary separating it from this nucleus. This suggests at least that the pulvinar of Primates is to be regarded as a differentiated portion of the lateral nucleus of lower forms. A study of the thalamus of a primitive lemuroid such as *Chirogaleus* or *Microcebus* would probably go far to settling this question of the homologies of the pulvinar, especially as the work of Kornyey (16) indicates that in general development and form the lateral geniculate body of *Chirogaleus* closely resembles that of *Tupaia*. It is unfortunate that Woollard, in his recent paper on the brain of *Tarsius*, did not give further details of this important region in that interesting animal which in many features of the brain appears to represent a structural link between the Tupaioids and Lemuroids. He states that in *Tarsius* "the pulvinar is well developed," but he gives no account of it.

It should be noted that, from its close association with the dorsal nucleus of the lateral geniculate body and its penetration by fibres of the optic tract (some of which probably terminate therein), it is not unlikely that the pars posterior of the lateral nucleus has been regarded by some authors as a part of the lateral geniculate body in some animals. Such a misconception will certainly lead to erroneous conclusions when experimental observations of lower mammals are applied to Primates.

Corpus Geniculatum Laterale. (Pls. I–III, figs. 3–6, *C.G.L.*)

The size and elaboration of this body form a remarkable feature of the thalamus of *Tupaia*. The two generally recognised elements, dorsal and ventral nuclei, are readily distinguished and both (but more especially the dorsal) are conspicuously developed. The dorsal nucleus extends in this transverse series from section 49 back to section 154, while the ventral element can be seen between sections 63 and 106. The dorsal nucleus consists generally of large, rounded, deeply staining cells, closely packed together. Anteriorly, lamination of the cells is indistinct, but in the greater part of its extent it is very clear. Rostrally, the dorsal nucleus appears as a small collection of cells at the upper and outer angle of the thalamus, situated immediately lateral to the anterior attenuated extremity of the pars posterior of the lateral nucleus, and covered by the optic tract. Traced caudally, its lower end, where the cells forming it are rather smaller than elsewhere, extends ventrally down the lateral margin of the thalamus. At section 87 it starts to enlarge somewhat rapidly and comes to form a large lenticular body lying vertically against the lateral thalamic margin, and attaining its greatest size in transverse section at section 107 (Pl. II, fig. 5). Here the lamination is particularly distinct. The lateral part of the nucleus is formed of a layer of large polygonal cells somewhat obscurely separated into two laminae, and two (more distinct) laminae of the same cell type are found on the medial aspect. At the upper pole, the medial and lateral laminae become continuous with each other. Between these layers of large

cells and occupying the centre of the dorsal nucleus is a core of small, rounded and lightly staining cells. These extend down to the ventral pole of the nucleus and here serve to link up the ventral extremities of the large-celled laminae. This central mass of small cells appears rostrally first in section 96. More caudally, the dorsal nucleus of the lateral geniculate body becomes pushed down into a more ventral position by the increasing size of the lateral nucleus above it, and, further back, by the appearance above the latter of the pretectal nucleus. Traced back, the inner layer of large cells begins first to disappear, so that at section 134 (Pl. III, fig. 6) it becomes dwindled to a short, undivided layer forming the upper half of the medial border of the dorsal nucleus, while below it are the remains of the small-celled central part. The caudal extremity of the dorsal nucleus is situated immediately dorso-lateral to the anterior part of the medial geniculate body.

The ventral element of the lateral geniculate body consists of cells which are relatively more lightly stained and not nearly so densely packed together. They are medium and fairly even in size, mostly triangular or fusiform in shape and with well-marked processes. It commences rostrally immediately ventral to the dorsal element and lateral to the lateral extremity (in this plane) of the reticular nucleus. It rapidly extends downwards in the concavity of the optic tract and by section 74 becomes a large mass. At section 69 it is seen to be separated by a clear band into two parts, medial and lateral, of which the former appears in intimate relation with the reticular nucleus. It is possible that this medial portion corresponds to the corpus pregeniculatum described in higher mammals. By section 74 the two parts have become fused together. The ventral element reaches its greatest size in transverse section approximately at section 83 (Pl. II, fig. 4). More posteriorly, it shrinks and is pushed on to the ventral aspect of the thalamus, where it lies immediately lateral to the pes pedunculi and the corpus subthalamicum.

The lateral geniculate body is covered laterally by the massive optic tract, from the medial aspect of which bundles of medullated fibres enter it. Those passing into the ventral nucleus enter mainly at its ventral extremity, and the impression is gained that not all of these terminate in the ventral nucleus but that some pass through to reach the dorsal nucleus. The latter is penetrated by better defined fasciculi which give it a laminated appearance. Numerous bundles of fibres emerge from the dorso-medial extremity of the ventral nucleus and pass towards the tectal region, and the dorsal nucleus appears to be similarly related to the pretectal nucleus. Gurdjian notes that, in the rat, the ventral nucleus is in intimate synaptic relations with the zona incerta and he believes that it is likewise associated with Meynert's commissure. These sections of the thalamus of *Tupaia* offer no positive evidence on these points. There is at least nothing here to compare with the condition in the brain of *Macroscelides*, in which a very conspicuous number of medullated fibres run from the medial aspect of the lateral geniculate body and converge into the ventral medullary lamina to pass towards the zona incerta, and apparently

correspond to the fasciculus geniculatus descendens described by Beccari in reptilian brains.

The transverse sections of the thalamus do not allow the geniculo-cortical fibres to be followed into the cortex.

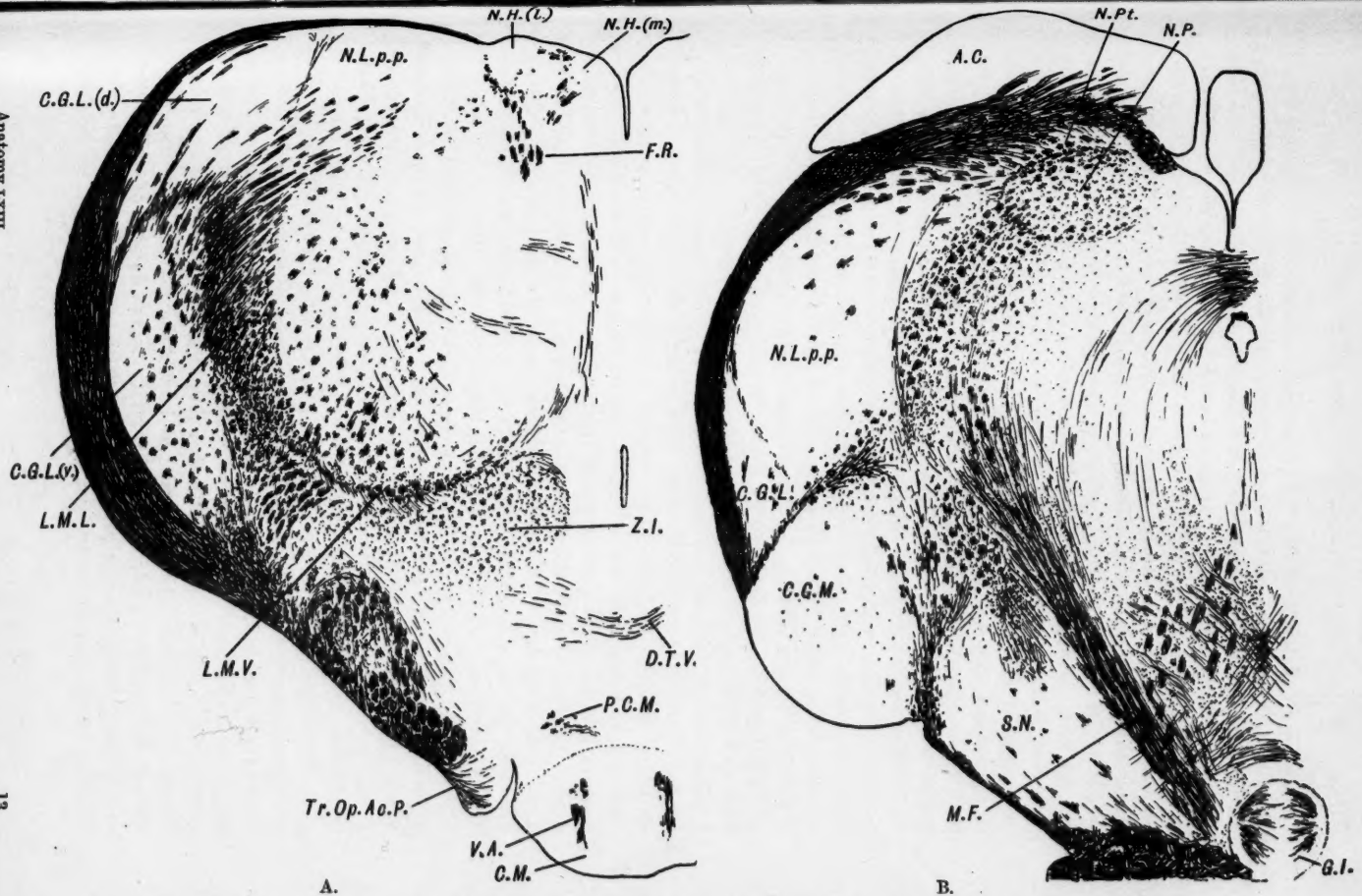
The great extent, both antero-posteriorly and dorso-ventrally, of the lateral geniculate body in *Tupaia* is very evident from the above description and from the plate-figures. This feature might be compared with the primitive condition found in reptilian brains, in which the body extends throughout the greater part of the thalamus in a sagittal direction except that the differentiation of the dorsal nucleus must be regarded as a progressive character. The ventral nucleus is large, as might have been inferred from the conspicuous size of the anterior colliculus, for it has been shown that this part of the geniculate body is pre-eminently connected with the mid-brain and is not projected on to the cortex cerebri (Kappers, Minskowski, Winkler, Woollard). But, even so, the ventral nucleus is not so large as the dorsal nucleus. The latter extends antero-posteriorly through practically the caudal two-thirds of the thalamus, while the ventral nucleus is limited to the middle third only. Moreover, in the middle of its length (Pl. II, fig. 5), the dorsal nucleus in cross-section covers a larger area than does the ventral nucleus in any part of its extent. Woollard's(28) statement (taken by itself) that in *Tupaia* "the lateral geniculate body has a small dorsal nucleus" is therefore somewhat misleading. Moreover, the differentiation of the dorsal nucleus is well advanced. It shows medial and lateral laminae of large cells connected together dorsally but not ventrally, which clearly represent the medial and lateral laminae described by Woollard in *Tarsius* and other Primates. Further, there is a central undifferentiated core of small cells which may be considered as the primordium out of which the "central area" described by Woollard in the Primates may have been developed. It is interesting to note that this central area in Primates is regarded as the site of termination of the macular fibres of the optic tract. The elaboration of the lateral geniculate body in *Tupaia* is consonant with the large optic nerves and tracts, the great size of the anterior colliculus, the elaboration of the oculomotor nucleus(4), and, above all, with the differentiation and surface extent of the area striata of the cerebral cortex. Kornyey's recent work on the comparative anatomy of the lateral geniculate body in Mammals indicates that this nucleus in the primitive lemuroid, *Chirogaleus*, bears a close resemblance to that of *Tupaia*. In *Chirogaleus* the rotation and ventral displacement of the geniculate body which has occurred in most lemuroids and in the Anthropoidea is hardly seen, so that, as in *Tupaia*, the free surface looks more laterally than ventrally. In section it is oval, and, in the more rostral planes, reniform with a medially directed concavity. Of a laminated structure, practically nothing is found, and its agreement with the general primate type is mainly expressed by the fact that a layer of large cells appears at the lateral border corresponding to the "ventral crest of large cells" described in other lemurs and in higher Primates. This layer of large cells appears to correspond

to the lateral laminae of large cells described in the dorsal nucleus of *Tupaia*. The griseum pregeniculatum was not found in *Chirogaleus*, and instead of this there appears at the ventro-oral pole a mass of cells in which the ventral nucleus of the lateral geniculate body (found in lower mammals) may be distinctly recognised. The ventral nucleus is also present, and well developed, in the brain of *Tarsius* (28). It thus appears that a structural transition from the type of lateral geniculate body in *Tupaia* to that in *Chirogaleus* would be effected merely by the diminution of the ventral element.

Nucleus Pretectalis. (Text-fig. 3 B, Pl. II, fig. 5, Pl. III, figs. 6 and 7, *N.Pt.*)

This is a nucleus which is particularly conspicuous and circumscribed in *Tupaia*, and is situated at the dorsal surface of the thalamus projecting from under cover of the anterior margin of the anterior colliculus. No account of a nuclear mass closely resembling this in the characters of the constituent cells has been found in accounts of other mammalian brains, but it occupies a position corresponding to that in which the pretectal nucleus, as described by Tsai (24), is found in the opossum's brain. It begins rostrally at section 111 at the dorsal surface of the thalamus as a small group of cells between the dorso-medial extremity of the pars posterior of the lateral nucleus and the habenular nucleus, and immediately dorsal to a collection of small cells forming the posterior nucleus of the thalamus. A few sections more caudally, it becomes clearly divided into two parts, a dorsal or large-celled element and a ventral or small-celled element. It rapidly enlarges and displaces the lateral nucleus laterally and ventrally. It reaches its largest size approximately at section 134 (Pl. III, fig. 6). Here the two elements are very distinct, but are not separated by any cell-free zone. In the dorsal part the cells are large, angular and fusiform, deeply stained, and with many and well-stained processes which interlace so as to give a very characteristic reticulated appearance. The ventral part consists of quite small cells, lightly staining, and mainly fusiform and triangular in shape. The whole nucleus becomes displaced laterally by the deeper strata of the anterior colliculus. Caudal to section 134 it diminishes in cross-section rather rapidly, and by section 170 the small-celled element has become indistinct, but a few of the characteristic large cells may be traced back to a considerable distance, forming a minute group on the dorsal aspect of the medial geniculate body.

In fibre preparations, large numbers of fibres from the dorsal extremity of the optic tract can be seen to penetrate into the pretectal nucleus. The size of the tract in this position, however, is perhaps too large to suppose that it here consists of retinal fibres only, and by analogy with other forms it may be inferred that these fibres terminating in the pretectal nucleus are at least mainly geniculo-pretectal fibres. The ventral aspect of the nucleus is in relation with numerous small bundles of fibres which surround and mark out the nucleus posterior and which appear to bring the pretectal nucleus into relation with the ventral thalamic nuclei and perhaps with the medial



Text-fig. 3. Transverse sections through the thalamus of *Tupaia minor* (second series, iron haematoxylin). A. At level of origin of fasciculus retroflexus. B. Through the nucleus pretectalis and nucleus posterior thalami.

lemniscus. The determination of the homologies of this nucleus presents some difficulties. Cajal (2) describes a nucleus prebigeminalis in the thalamus of the mouse and rabbit which is situated in a corresponding position and which is related to the optic tracts and also receives collaterals from the medial lem niscus. From his description and figures there seems little doubt that his nucleus prebigeminalis corresponds to the nucleus pretectalis + nucleus posterior thalami described here in *Tupaia*. Similarly, Haller's nucleus pretectalis which he describes in *Mus* is equivalent to Cajal's prebigeminal nucleus. In the rat, Gurdjian recognises the pretectal area as an undifferentiated mass of grey matter rostral to the tectum and continuous (with a very gradual zone of transition) with the lateral nucleus in front. This area seems to correspond to the pretectal nucleus described for *Tupaia*, while the posterior nucleus of the latter is homologous with the posterior nucleus distinguished by Gurdjian. Tsai describes the pretectal nucleus in the opossum in the same relative position, and states that it consists of small round and pyramidal cells. But it seems from his description and from its characteristic appearance in the figures of Weigert preparations that his pretectal nucleus also includes the posterior nucleus of *Tupaia*. It is obviously important to note these different connotations of the name "pretectal" when comparisons are made between one brain and another. Tsai concludes that some of the mesencephalic fibres of the optic tract end in his nucleus pretectalis, and that probably some diencephalic optic fibres also reach it by way of the dorsal division of the lateral geniculate body. He traces into it fibres from the lateral geniculate body and from the anterior colliculus, and he further notes the presence of a tractus pretecto-nigralis which descends from his pretectal nucleus to the tegmentum and especially to the substantia nigra. This appears to be identical with the fasciculus pretectalis descendens described first by Beccari in *Varanus* and later by Huber and Crossby in *Alligator*. In the rat and the opossum, the nucleus pretectalis as described for *Tupaia* appears to be but feebly differentiated. In *Tupaia*, however, the differentiation is marked, and this is perhaps in harmony with the high level of organisation of other elements of the visual apparatus of the brain.

Edinger, de Lange (17), Haller (12), and Huber and Crossby (14) have described a pretectal nucleus in reptiles which seems to be homologous with the mammalian pretectal nucleus (? pretectal n. + posterior n. of *Tupaia*). Edinger has established the existence of a large fibre tract linking up the nucleus rotundus with the nucleus praetectalis in reptilia, and has also demonstrated the presence of a geniculo-praetectal tract. De Lange emphasises the intimate relation between the pretectal nucleus and the substantia grisea of the tectum. In the alligator, Huber and Crossby describe the pretectal nucleus as consisting of medium-sized cells and as being "rather sharply delimited by the surrounding fibre tracts." Further, they describe as lying "dorso-medial to the nucleus pretectalis and not sharply separated from it...a small group of rather large-sized cells," Edinger's nucleus spiriformis. This group is in intimate fibre relation with the pretectal nucleus. From this account it might be suggested

that the nucleus spiriformis corresponds to the large-celled dorsal element of the pretectal nucleus in *Tupaia*, while the reptilian pretectal nucleus represents the ventral small-celled element. But whatever may be the precise homologies, it seems clear that the pretectal nucleus has a very ancient history.

The suggestion has been made that the nucleus pretectalis is homologous with the pulvinar of the primate thalamus. This suggestion is based mainly on the relation of the pretectal nucleus to the fibres of the optic tract. But the same argument applies equally well to the pars posterior of the lateral nucleus and, in addition, it is probable that the latter element has cortical connections, while pretecto-cortical fibres have not been observed. But it may be said that if the pars posterior of the lateral nucleus is the only homologue of the pulvinar, then there is nothing in the primate brain which might be homologised with the pretectal nucleus of lower mammals. Either, then, the pretectal nucleus is not represented at all in the primate thalamus, or, alternatively, the pulvinar is of a composite origin in the formation of which both the pars posterior of the lateral nucleus and the pretectal nucleus take part. The composite nature of the pulvinar is suggested by Pines' description of this element in *Lemur Catta*. This author divides the pulvinar of *Lemur* into two main parts, a latero-dorsal and a ventro-medial portion. The former consists of cells which are larger and more deeply stained, and irregularly distributed in groups and nests. The cell form is irregular, rounded or angular, with well-marked processes. The cells of the ventro-medial portion are more diffusely spread out. It is uncertain whether in *Tupaia* the size and differentiation of the pretectal nucleus are associated with the differentiation of the telencephalic visual apparatus rather than with the enormous size of the anterior colliculus, for in *Macroscelides*, in which the anterior colliculus is very large while the visual cortex and dorsal element of the lateral geniculate body are feebly developed, the pretectal nucleus is quite conspicuous though it is not relatively so large as it is in the tree-shrew. Here, again, a detailed examination of the thalamus of primitive primates such as *Tarsius* and *Microcebus* would probably supply evidence of value. It may be noted here that the posterior nucleus of the thalamus (which has been included by several authors in the term "pretectal nucleus") is small and not sharply defined in *Tupaia* (*vide infra*), whereas in *Macroscelides* it attains to a large size and is well differentiated.

Nucleus Posterior. (Pls. II, III, figs. 5, 6, *N.P.*)

This nucleus, which is poorly defined in toluidin blue sections, consists of a group of small cells somewhat diffusely scattered and appearing rostrally at section 106 ventro-medial to the lateral nucleus and lateral to the nucleus parafascicularis. A few sections more caudally it becomes covered dorsally by the pretectal nucleus, but separated from it by a relatively cell-free band. At section 136 it becomes indistinct. In fibre-stained sections the nucleus is better defined, being surrounded and penetrated by numerous small bundles of fibres which appear to extend upwards from the region of the mesial fillet.

There is no conclusive evidence that it receives terminals from the optic-tract system. This corresponds with Tsai's observation that the nucleus posterior of the opossum's brain appears to receive no optic fibres. But, judging from this author's description and figures, it is not certain whether his nucleus posterior is homologous with that here described. It seems probable that his pretectal nucleus includes the element called nucleus posterior in *Tupaia* and that he applies the term nucleus posterior to a diffuse mass of cells situated more ventrally. In Gurdjian's description of the rat's thalamus there is a nucleus posterior which closely corresponds to that described here in *Tupaia*, and he states that it receives fibres from the superior thalamic radiation and the optic tract and that it is also connected with the tectum. My observations on the thalamus of other insectivores indicates that this element is very variable in its development in different species, and it is no doubt this variability which makes comparison of this region in different animals so difficult. We were in some doubt as to whether it would not be advisable to group this nucleus posterior together with the nucleus pretectalis described above as a single unit to correspond with the nucleus pretectalis described in some other mammals by different authors. But it was decided to separate them because of the clear distinction in cyto-architecture and myelo-architecture of the two cell masses. Optic-tract fibres could be traced in large numbers into the substance of the pretectal nucleus of *Tupaia* but not further with any certainty into the posterior nucleus.

Corpus Geniculatum Mediale. (Pl. III, figs. 6, 7, *C.G.M.*)

This body first appears rostrally at section 129 as a collection of pale scattered cells lying immediately medial to the ventral half of the lateral geniculate body in this section, between it and the zona incerta medially. At section 138 it begins to project on the surface of the thalamus, producing a superficial elevation. The nucleus extends back to section 196 and reaches its maximum development in transverse section at about section 158 (Pl. III, fig. 7). It is in relation dorsally with the lateral geniculate body for a little more than its rostral third. It has not been found possible to analyse the medial geniculate body of *Tupaia* into separate elements, for its structure is relatively homogeneous though there is a tendency perhaps for the cells to be more closely arranged on the lateral than on the medial aspect. This lack of differentiation is perhaps to be correlated with the diminutive size of the posterior colliculus and the apparently degenerate nature of the external ear of the animal. It is stated, also, that uniformity of structure of the medial geniculate body is a characteristic feature of the Primates.

Nucleus Ventralis. (Pls. I–III, figs. 3–6, *N.V.*)

The various elements of the ventral nuclear complex of the thalamus are not difficult to recognise, though, as will be pointed out, certain portions show a tendency to grade almost imperceptibly into neighbouring cell masses. Broadly speaking, the ventral nuclei are those collections of cells belonging to

the thalamus proper which lie ventral to the transversely running band of cells which forms the paracentral nucleus. While I have not found it possible to distinguish with confidence the component nuclei described by Gurdjian in the brain of the rat, especially his dorso-medial element, I have found it comparatively simple to apply the account given by Pines of the ventral nuclei in *Lemur* to those of *Tupaia*. Generally speaking, the constituent cells of the ventral nuclei are medium and large-sized, rounded, and staining uniformly and fairly strongly with toluidin blue. In most sections the nuclear groups stand out clearly because of the contrast between their characteristic cells and those of surrounding groups and because they are outlined by relatively cell-free bands. It is possible to distinguish anterior and posterior groups, each again subdivided into medial and lateral nuclei. These may be termed the antero-medial and antero-lateral ventral nuclei, and the postero-medial and postero-lateral ventral nuclei.

Rostrally, at section 31, immediately ventral to the antero-medial nucleus and close to the mid-line (but separated from the raphe cells here by a clear zone), a group of medium, rounded cells appears extending laterally and slightly dorsally, so that it forms a transverse oval. It is bounded laterally and ventrally by the n. reticularis, and medio-ventrally by a compact group of small cells extending out from the median raphe, the nucleus reuniens. This is the antero-medial ventral nucleus (Cajal's ovoid mesial nucleus, Pines' nucleus *vtm.*, Gurdjian's n. ventro-medialis). Lateral to this nucleus lies a more diffuse group of smaller and rather more fusiform cells with their axes lying transversely. This group, which represents the anterior extremity of the antero-lateral ventral nucleus (Cajal's intermediate ventral nucleus or n. triangularis, Pines' nucleus *vtl.*, and the anterior part of Gurdjian's nucleus ventralis), extends in a dorso-lateral direction, covered dorsally by the antero-ventral nucleus and the nucleus lateralis B. The boundary between it and the latter is not distinct in the caudal planes. Traced caudally, the nuclei enlarge and are not always to be separated from each other. At section 54 they become covered above by a conspicuous band of elongated cells running transversely from the mid-line, the nucleus paracentralis. The antero-lateral ventral nucleus in many sections blends with the lateral extremity of the paracentral nucleus, and together they may run without apparent interruption into the ventral aspect of nucleus lateralis B. At section 60 the medial and lateral nuclei become more obviously separated by a narrow band of cells turning down from the lateral extremity of the paracentral nucleus. At section 68 the nucleus paracentralis starts to shrink, and an irregular and very ill-defined mass of small cells appears in the position of its lateral extremity. These become more extensive in their distribution more caudally, and would appear to correspond (at least in part) to the nucleus ventralis pars dorso-medialis described by Gurdjian. The boundaries of this irregular collection of cells are, however, most indefinite. At section 71 the antero-medial ventral nucleus begins to disappear, or, rather, it seems to be pushed laterally to become joined

up with the antero-lateral ventral nucleus which thus grows much larger and more compact. The individual cells of this nucleus also become distinctly larger at this level. Laterally, however, the antero-lateral ventral nucleus expands, and fades away into a diffuse group of smaller cells which stretch out to the medial aspect of the lateral geniculate body but separated from the latter by the lateral medullary lamina. This small-celled dorso-lateral extension of the antero-lateral ventral nucleus evidently corresponds to Cajal's ventro-lateral or main sensory nucleus, and it is here that the main bundles of the medial lemniscus appear to terminate[1]. We were in some doubt as to whether this portion should be separated from the medial part of the antero-lateral ventral nucleus (Cajal's n. triangularis) as Cajal has done. But the two parts grade into one another imperceptibly, and Cajal himself notes in discussing his triangular nucleus that "dans certaines préparations, elle semble constituer un simple lobe interne du noyau sensitif."

At section 79 the antero-medial ventral nucleus has disappeared from its position close to the mid-line. At section 88, however, a similar group of large rounded cells appears again in this position, representing the rostral end of the postero-medial ventral nucleus (Pines' nucleus *vb.*). This nucleus, in the anterior part of its extent, is connected with that of the opposite side by a small commissural band of cells representing Gurdjian's nucleus commissuralis interventralis. The lateral part of the antero-lateral ventral nucleus extends back to section 98, forming a rather ill-defined crescentic mass with its concavity dorsally, and bounded laterally by the small-celled ventral nucleus of the lateral geniculate body and ventrally by the remains of the nucleus reticulatus. It breaks away laterally into irregularly disposed small cells which reach out to the lateral medullary lamina. Caudal to section 98, a well-defined group of characteristic large, rounded and well-stained cells appears, immediately lateral and somewhat ventral to the postero-medial ventral nucleus. This is the postero-lateral ventral nucleus (Pines' nucleus *va.*). It forms a very circumscribed nucleus usually fairly distinct from the medial nucleus (which is composed of the same type of cells), though in some sections a transition zone may be seen linking up the two nuclei. They both lie immediately on the dorsal aspect of the medial lemniscus which here runs transversely medialwards to curve ventrally close to the mid-line. The medial element disappears at section 108, or merges there with the lateral element, being displaced from its medial position by the relatively more dorsal position of the medial lemniscus system in the more caudal planes. At section 121 the postero-lateral ventral nucleus becomes very indistinct, and its cell elements become smaller and less regular.

The termination of the main bundles of the medial lemniscus can be seen in the ventral nucleus, especially in the lateral part where the lateral extremity of the antero-lateral ventral nucleus breaks away into an irregular mass of

[1] Friedemann labels this region in the thalamus of *Cercopithecus* as "Übergangzellen von *va* in *lb*."

smaller cells. This lateral region corresponds to Cajal's main sensory nucleus as has already been indicated. The ventral nuclei are also brought into relation with the thalamic radiations. In the rat, Gurdjian found very evident connections between the ventral nucleus and the cortex. Sachs, working experimentally, found connections between the ventral nucleus and the gyri pre- and post-crucialis, sigmoidalis, lateralis, and suprasylvius medius of the cat's brain. He further found that injury to the nucleus ventralis in the Macaque monkey led to a degeneration of fibres downwards in the posterior longitudinal bundle, with collaterals to the nuclei of the cranial nerves V, VI, VII and X. He thus believes that the posterior longitudinal bundle, in addition to ascending fibres, contains descending fibres which originate in the ventral nucleus of the thalamus. According to Probst, some of the fibres of the superior cerebellar peduncles terminate in the ventral nucleus.

Nucleus Dorso-medialis (Pls. I, II, figs. 3, 4, *N.Md.*) (Cajal's intermediate dorsal nucleus, the dorsal part of the medial nucleus of Winkler, the dorsal limb of the nucleus arcuatus of Munzer and Wiener, "medialer Hauptkern" of Friedemann).

This nucleus consists of medium rounded cells of even shape scattered rather sparsely but forming a group which is usually fairly well defined and enclosed by clear medullary laminae. It would appear that this nucleus represents in the main the "mediale fibröse und grosszellige Partie des medialen Hauptkerns" described by Friedemann and Pines in the brains of *Cercopithecus* and *Lemur*, while the smaller-celled element which, in *Cercopithecus*, attains to such a conspicuous development, is represented in *Tupaia* by the ill-defined area of small scattered cells lying lateral to the dorso-medial nucleus between it and the lateral nucleus and which may here be called the nucleus dorso-medialis lateralis (Pl. I, fig. 3, *N.Md.l.*).

The dorso-medial nucleus, as here defined, appears rostrally at section 48 as a few cells lying close up against the nucleus dorsalis raphae and immediately beneath the lateral part of the parataenial nucleus, above the caudal remnant of the antero-medial nucleus. By section 59 (Pl. I, fig. 3) the nucleus has become well defined, and at this level the median raphe cells have disappeared so that the two dorso-medial nuclei appear to be closely related to each other across the mid-line (forming what Gurdjian calls the nucleus commissuralis intermedio-dorsalis). At this level, also, the nucleus comes into relation ventrally with the n. paracentralis. At section 83 (Pl. II, fig. 4) it is more diffuse and is in relation ventro-laterally with an irregular mass of small cells which becomes developed at the lateral extremity of the paracentral nucleus and which evidently corresponds to the dorso-medial part of the ventral thalamic nucleus as described by Gurdjian in the rat's brain. Eventually, at section 105, the dorso-medial nucleus becomes displaced medially by the appearance of the fibres of the fasciculus retroflexus and disappears. According to Gurdjian, this nucleus in the rat receives fibres from the intermediate

thalamic radiation, and an indication of these fibres may be seen in the myelin-stained sections of the *Tupaia* brain.

Munzer and Wiener describe the dorso-medial nucleus as the dorsal limb of a large nucleus arcuatus of which the ventral limb is formed by the ventro-medial nucleus. According to these two authors, these two nuclei become united in the rabbit by a vertically disposed column of cells at the anterior end of the thalamus. In this way a large curved nucleus is formed with the convexity and the summit of the curve directed rostrally. In my sections of the tree-shrew's brain, I have not been able to detect any union between the dorso-medial and ventro-medial nuclei, though it is possible that a parasagittal section of the thalamus might indicate such a connection. It may be noted that these two nuclei are composed of similar types of cells.

Nucleus Parafascicularis. (Pl. II, fig. 5, *N.Pf.*)

As noted by d'Hollander (13) and Gurdjian (11), this appears to be merely the caudal extremity of the dorso-medial nucleus which is here altered in appearance by the penetration of the fibres of the fasciculus retroflexus. It is conspicuous for the close packing of its cells. As the nucleus descends ventrally through the thalamus in association with the bundle of Meynert, it comes into relation laterally with a triangular mass of cells which lies immediately dorsal to the caudal traces of the paracentral nucleus and, below the latter, to the posterior medio-ventral nucleus (Pl. II, fig. 5). This cell group, which first appears in section 103 (Pl. II, fig. 5), enlarges rapidly and, by reason of the fairly dense packing of its cells, forms a conspicuous feature. It becomes linked up with the nucleus parafascicularis, and, indeed, may be regarded as a part of this. It occupies a position corresponding to that of the centre median nucleus of Luys which attains such a marked development in the anthropoidea. Apart from this group of cells, there is nothing in the thalamus of *Tupaia* which can be homologised with the centre median nucleus. Indeed, it is said that the latter is only to be found in Primates. It is large in *Cercopithecus* (Friedemann), quite evident in *Hapale* (Brunner and Spiegel) and *Tarsius* (Woollard), and present in *Lemur* (Pines). Sachs, however, says that the centre median nucleus in *Lemur* cannot be distinctly recognised, and he records it as being conspicuous in *Lepus, Camelus, Phocaena,* and *Macropus,* while it is absent or difficult to distinguish in *Canis, Felis, Herpestes, Lutra, Nasua, Talpa, Mus, Cavia, Sus, Bos, Equus, Dasypus,* and *Perameles.*

Nucleus Centralis (Pls. I, II, figs. 3, 4, *N.C.*) (Cajal's median rhomboid nucleus) and *Nucleus Paracentralis* (Pls. I, II, figs. 3, 4, *N.Pc.*) (Cajal's falciform nucleus, Munzer and Wiener's lateral extension of the nucleus of the mid-line, Pines' nucleus submedialis).

In many sections the nucleus centralis forms a conspicuous mass of small round cells densely packed together in the mid-line, but its rostral and caudal limits are very indefinite. At about section 36 it appears as a dense collection

of cells in the median raphe at the ventral extremity of the nucleus dorsalis raphae and lying above the caudal part of the antero-medial nucleus. These cells stretch laterally and slightly dorsally towards nucleus lateralis B. The cells of the central nucleus differ in appearance by their rounded shape and somewhat larger size from the small vertically disposed fusiform cells which lie in the median raphe above and below. Caudally the central nucleus enlarges and takes on a very characteristic diamond shape, while the lateral extensions, forming the paracentral nuclei, become longer and more conspicuous. The central nucleus thus comes to form the centre of a cruciform arrangement of cells of which the horizontal limb is formed by the paracentral nuclei on both sides and the vertical limb by the median raphe cells above and below. Intimately associated with the central and paracentral nuclei are numerous commissural fibres which in many sections collect to form a clear cell-free band dividing the central and paracentral nuclei into dorsal and ventral moieties. The more dorsal of these commissural fibres appear to be related to the anterior ends of the lateral nuclei, and the more ventral to the antero-lateral ventral nuclei and nucleus lateralis B. At section 59 (Pl. I, fig. 3) the central nucleus lies midway between the dorsal surface of the thalamus and the upper limit of the third ventricle. Dorsally it extends upwards in many sections into the nucleus dorsalis raphae and ventrally it is in relation with the median raphe cells which here separate the antero-medial ventral nuclei from each other. Laterally, at this level, the paracentral nucleus extends outwards and upwards, separating the dorso-medial nucleus above from the antero-medial ventral nucleus below. Posteriorly, the lateral extremity of the paracentral nucleus becomes diffuse and gradually develops into a poorly defined but extensive mass of small cells which come into intimate relation with the small-celled lateral extension of the antero-lateral ventral nucleus.

Nucleus Reuniens. (Pl. I, fig. 2, *N.Re.*)

At section 16 a few scattered cells of medium size appear in the mid-line ventral to the nucleus dorsalis raphae (nucleus paraventralis anterior) and immediately dorsal to the upper end of the ventricular cavity, between the medial ends of the antero-medial nuclei. By section 30 these cells have increased in number and become more densely packed together, and show a tendency to a division into two bilateral halves. They become displaced ventrally by the appearance of the nucleus centralis and nucleus rhomboidalis, and by section 45 they can no longer be recognised as a distinct unit.

Nucleus Rhomboidalis. (Pl. I, fig. 3, *N.Rh.*)

At section 43 this group of cells appears in the mid-line between the anterior end of the nucleus centralis above and the nucleus reuniens below. It forms a close collection of small cells which, however, cannot be sharply distinguished from the nucleus centralis anteriorly. Caudally it extends in a ventral direction, between the antero-medial ventral nuclei. By section 60 it can no longer be identified.

Nucleus Dorsalis Raphae (Pl. II, fig. 4, *N.D.R.*) (Gurdjian's nucleus paraventricularis).

This commences at section 14 as a ventral extension into the mid-line of the medial parataenial nucleus. More caudally it comes to lie between the dorso-medial nuclei, forming two masses on either side close up against the mid-line. At section 79 it forms a dense undivided collection of cells lying in the mid-line and extending ventrally into continuity with the nucleus centralis. At section 97 it retracts dorsally and forms two separate clumps of cells on either side of the median plane immediately ventral to the medial habenular nucleus (= Gurdjian's nucleus paraventricularis posterior). It disappears close to the point where Meynert's bundle comes off and loses its identity or becomes continuous with the nucleus parafascicularis.

Nucleus Subthalamicus. (Pls. II, III, figs. 4–6, *C.L.*)

This nucleus is first to be seen rostrally at section 76 as a small collection of darkly staining cells at the middle of the dorsal surface of the pes pedunculi. Traced caudally, these cells spread medially and laterally to form the characteristic elongated corpus subthalamicum. They differ in their size and staining reaction from any other cells in the neighbourhood. The cells on the whole are oval with their transverse axes disposed transversely. The nucleus extends laterally up to the ventral nucleus of the lateral geniculate body but separated from this by a clear zone. Medially it extends towards the hypothalamus. After section 105 it diminishes rather rapidly and its cells become more scattered, but more caudally again at section 125 it becomes larger and many of its cells, which here are more angular and irregular in shape and show well-marked processes, are scattered among the fibres of the pes pedunculi. They also show a tendency to congregate at the inner side of the pes, close to the interpeduncular ganglion. The nucleus disappears at the level of the exit of the third nerve fibres except for some scattered cells among the fibres of the pes.

Nucleus Opticus Tegmenti. (Pl. III, fig. 6, text-fig. 3 A, *N.Op.T.*)

This nucleus consists of small angular and fusiform cells situated at the medial end of the pes pedunculi, first visible in section 123 and extending caudally to section 140. It forms an isolated group of cells and, as Tsai has pointed out, may be distinguished from the substantia nigra and the nucleus tegmentalis ventralis by cell-free zones and by the characters of its constituent cells. Caudally it becomes displaced up above the medial end of the pes and comes into close relation with the substantia nigra and immediately lateral to the issuing fibres of the third nerve. In it terminate the fibres of the posterior accessory optic tract (tractus peduncularis transversus).

HYPOTHALAMUS

A detailed cyto-architectural study of this difficult region would be out of place in the present communication, partly because the functional significance of the various "nuclei" which have been described is so little understood and

partly because they have not the same value from the point of view of comparative anatomy as the nuclei of the optic thalamus proper. Several cell groups have however been recognised and merit a brief mention here.

Nucleus Magnocellularis Hypothalami. (Pl. I, fig. 2, *N.M.Hy.*)

By reason of its large and characteristic cells, this nucleus forms one of the most conspicuous elements in the hypothalamus of *Tupaia*. It has been described by Tsai(25) in the brain of the opossum, but Gurdjian does not recognise it in the rat. Rostrally it is first evident at section 6 where it appears close to the ependymal lining of the third ventricle and about midway between the dorsal and ventral surfaces of the thalamus. It is formed of roundish or polygonal cells, not very deeply staining, and rather larger than the cells found in the antero-ventral nucleus. They are densely packed together and tend to arrange themselves in vertical rows along the lateral walls of the third ventricle. The nucleus reaches its greatest development at section 17, where it forms on either side of the ventricle a club-shaped mass with a bulbous dorsal extremity reaching up towards the nucleus reuniens on a level with the anterior end of the nucleus filiformis, and an attenuated ventral extremity extending down almost to the dorsal surface of the optic chiasma but separated from the latter by a small mass of round cells close up against the mid-line which probably represents Gurdjian's nucleus ovoidus. By section 23 the ventral tail of the nucleus has disappeared to be replaced by scattered small cells corresponding to the anterior hypothalamic nucleus, and the cells of the remaining portion appear smaller and less compactly arranged. The nucleus finally disappears altogether at section 34 and its place is taken by the medial part of the filiform nucleus.

Nucleus Filiformis. (Pl. I, figs. 2, 3, *N.Fi.*)

This appears rostrally at section 23 as a collection of small cells lateral to the nucleus magnocellularis. When the latter disappears caudally, the small-celled group enlarges considerably and forms a conspicuous triangular mass immediately ventral to the antero-medial ventral nucleus, extending laterally to the ventro-medial extremity of the nucleus reticularis and caudally as far as the anterior end of the zona incerta.

Nucleus Hypothalamicus Lateralis. (Pl. I, figs. 2, 3, *N.Hy.L.*)

This is the interstitial nucleus of the medial forebrain bundle and does not form a well-defined cell group. It is found in the anterior part of the hypothalamus, lying between the nucleus ovoidus and anterior hypothalamic nucleus medially and the entopeduncular nucleus laterally. It consists of a region containing scattered cells of a rather larger size than those found in the hypothalamus generally.

Nucleus Hypothalamicus Medialis.

As seen in Pl. II, fig. 4 (*N.Hy.M.*), this nucleus caudally consists of an undivided mass of small cells lying close up against the walls of the third

ventricle. Anteriorly, however, it becomes divided into two groups, a nucleus hypothalamicus dorso-medialis above and a nucleus hypothalamicus ventro-medialis below (Pl. I, fig. 3).

Nucleus Tangentialis (Pl. I, figs. 1, 3, *N.T.*) (N. Supraopticus, Ganglion basale opticum).

This nucleus is very readily recognised by its characteristic cells. It is split into two quite separate halves in *Tupaia* by the large optic chiasma. Rostrally it appears on the dorsal aspect of the anterior margin of the chiasma on either side of the mid-line. Caudally it gradually extends laterally and finally disappears at the lateral margin of the chiasma at section 8. Considerably further back, at section 40, it reappears at the medial borders of the optic tracts where they are commencing to diverge from the chiasma. Finally the nucleus disappears again at section 60.

DISCUSSION

A study of the thalamus of *Tupaia minor* indicates (as might have been anticipated from a consideration of the gross anatomical features of the brain as a whole and the elaboration of the area striata of the cortex) that a large proportion of this body is made up of visual elements. Both the ventral and dorsal elements of the lateral geniculate body are very large, the pars posterior of the lateral nucleus is relatively conspicuous, and the pretectal nucleus is prominently developed. The large size of the pars posterior of the lateral nucleus is in harmony with Gurdjian's statement that this nucleus in the rat receives terminals from the optic tract, and adds strength to the suggestion that it is this element which represents the pulvinar in higher forms. The lateral nucleus elements A and B evidently represent in a simplified form the cell masses which become so highly elaborated in those mammals which possess a highly organised and complex neopallium. While the element A is well defined and consists of cells identical in type with those which form the pars posterior of the lateral nucleus, the element B is more irregular, consists of cells of a different type, and, caudally, merges indistinguishably with the lateral extension of the ventral nucleus. The ventral nucleus can be divided into elements which appear to correspond well with those which have been described in the thalamus of *Lemur* by Pines. They are separated from the dorso-medial nucleus above by the well-defined nucleus paracentralis. This horizontal band of cells serves to divide the thalamus into dorsal and ventral moieties very clearly. Posteriorly there is differentiated from the lateral end of the paracentral nucleus a small but conspicuous mass of cells which appears to represent the centre median nucleus which forms such a conspicuous structure in the brain of Primates. The dorso-medial nucleus is easy to define, and immediately lateral to the main element may be seen a collection of smaller cells which may be regarded as the forerunner of the relatively large nucleus to be

found in *Cercopithecus* and which Friedemann named the "medialer Hauptkern." Of the anterior group of thalamic nuclei, the antero-ventral and antero-medial nuclei are well developed, while the antero-dorsal nucleus is relatively diminished in size and shows an approximation to the primate form of this element in that its constituent cells are not relatively larger than those of the other elements of the anterior nucleus. The posterior nucleus, which corresponds to a part (at least) of the pretectal nucleus of many other writers, is small and ill-defined. No fibres from the optic tract could be traced into this nucleus. The medial geniculate body is not so prominent relatively as in many other lower mammals, and it was found to be homogeneous in its structure.

In general, then, the structure of the thalamus of *Tupaia minor* is in harmony with the structure of the brain as a whole. It is a matter of some interest that in the brain of such a primitive mammal the visual elements of the thalamus have attained to such a high level of differentiation, though such a condition might perhaps have been anticipated when it is realised that in reptilia generally the optic nerves and tracts are very large and the visual elements of the mid-brain and thalamus are already relatively well developed.

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DESCRIPTION OF PLATES I–III

Transverse sections through the thalamus of *Tupaia minor* from before backwards. (First series. Toluidin blue.)

Plate I.

Fig. 1. Section 2. Fig. 2. Section 23. Fig. 3. Section 59.

Plate II.

Fig. 4. Section 83. Fig. 5. Section 111.

Plate III.

Fig. 6. Section 134. Fig. 7. Section 158. (The numbers refer to the layers of the anterior colliculus.)

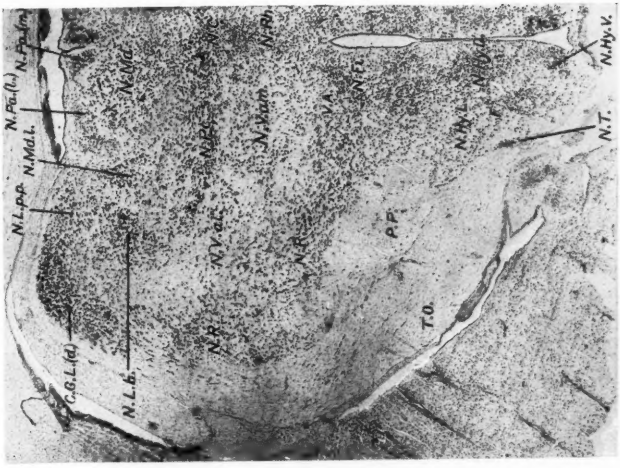

Fig. 3.

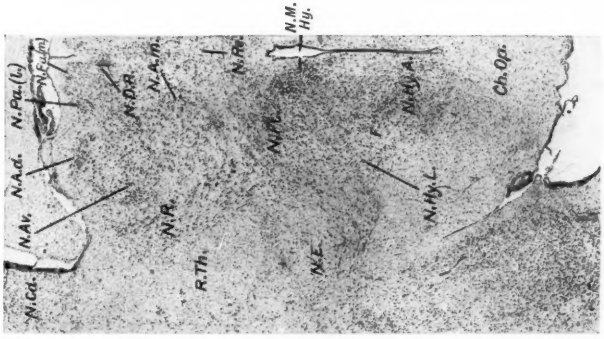

Fig. 2.

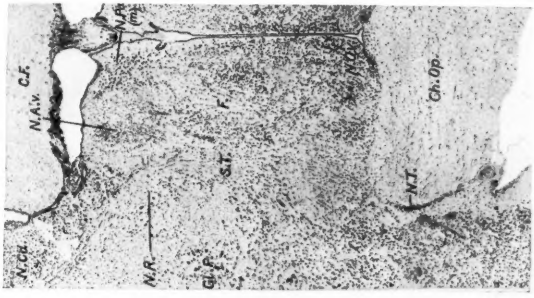

Fig. 1.

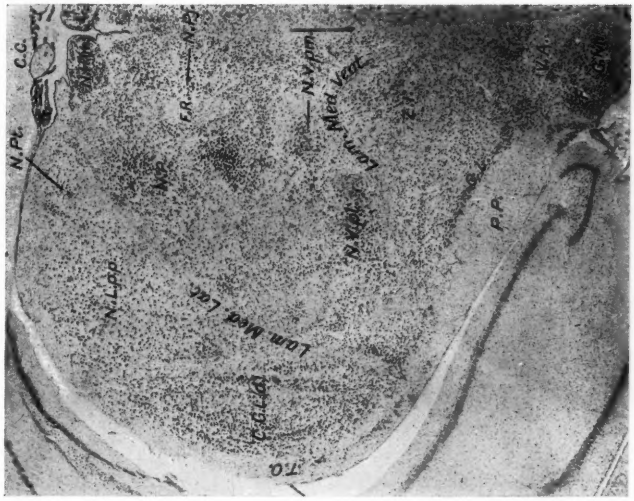
C.C.
N.Pt.
N.R.
T.R.
N.Pul.
Lam. Med. Vent.
N.Lpul.
Lam. Med. Lat.
C.G.L.(V)
T.O.
P.P.
V.A.

Fig. 5.

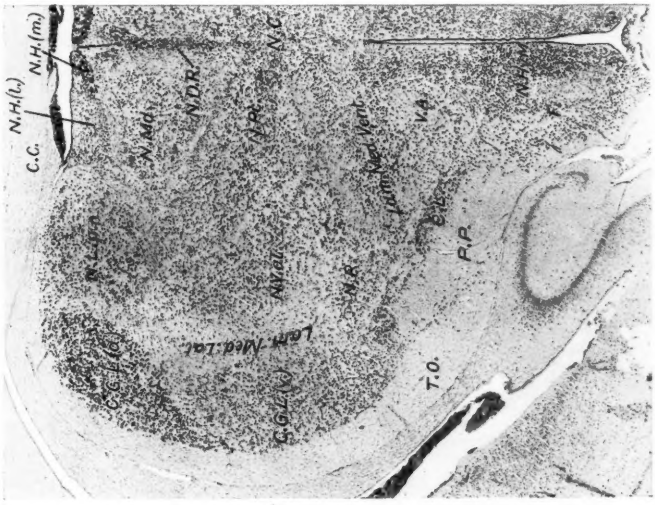
N.H.(l.)
N.H.(m.)
C.C.
N.Md.
N.D.R.
T.R.
N.C.
N.Lpul.
Lam. Med. Lat.
C.G.L.(V)
N.R.
Lam. Med. Vent.
V.A.
P.P.
T.O.

Fig. 4.

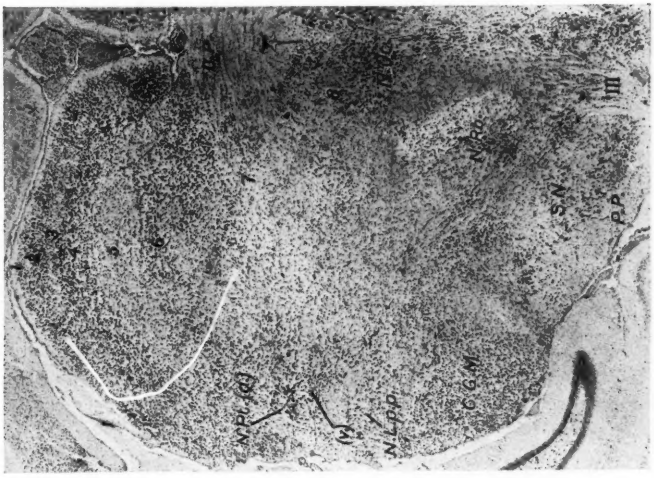

Fig. 7.

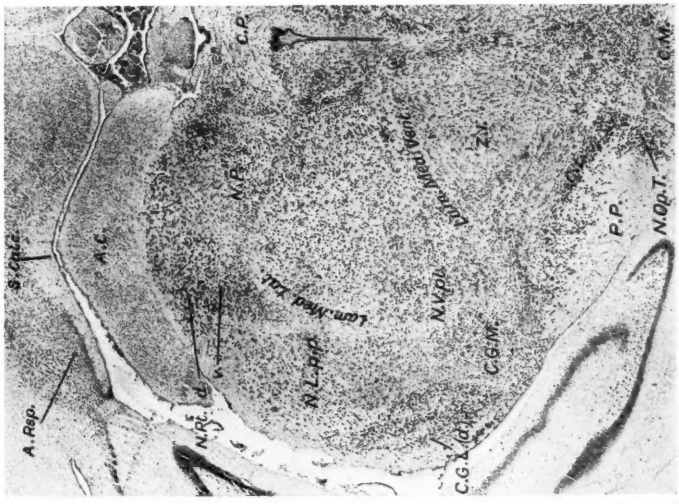

Fig. 6.

UNIV. OF MICH.

THE AUSTRALIAN ABORIGINAL BRAIN

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THE intrinsic interest of the aboriginal brain, the comparative rarity of studies of well-preserved specimens, and the probability that material will become more and more difficult to obtain, are sufficient reasons for the following notes.

The material likely to present itself at the Anatomical Department in an Australian city at this date must be always subject to the suspicion that it may not be derived from full-blooded aborigines. All the four brains that have been examined are said to be those of full-blooded aborigines, yet the specimen numbered three is open to suspicion. The suspicion is based not only on discrepancies in the pattern of the fissures, but also in marked differences in measurement. However, be this as it may, Brain 1 appears to be the most distinctive and it appears to repeat very faithfully the pattern of the brain numbered 4 in Duckworth's series. Duckworth remarked that this brain appeared to be the most primitive in his series.

In view of the few brains already described and the extreme unlikelihood that the numbers will ever be considerable, little value can be attached to percentage calculations. The comparison of drawings and photographs shows that the brain of the aborigine varies considerably, as do all brains, in regard to those fissures which are least stable. Though it may seem an extremely biassed procedure, perhaps most might be obtained from such a study as this by dwelling on the brain that seems most primitive in all features. Measurements of the length and depth of sulci, the frequency of single and bifid terminations, and so forth, are so variable that they seem useless. Moreover, it appears that no standard exists for any certain comparison. For instance, it seems quite misleading to compare a dolichocephalic brain numerically or in its detailed fissural pattern with any other brains, say European, unless these have been first standardised in regard to dolichocephaly or brachycephaly. A recent investigation by Kappers has shown that the Dutch brachycephalic brain is much more like a Chinese brain than it is like a Dutch dolichocephalic brain. Such an observation also invalidates many comparisons that have been made not only with European brains, but also with the brains of new-born, for in these any brachycephaly that is present is greater than when they are full grown. The anthropoids being mostly brachycephalic, the same criticism can be urged though with less force since the comparisons with these are confined to the more stable elements in the brain.

When this study was begun it was hoped that a description of the fissures based on their relations to the histologically differentiated areas of the brain

might be achieved. It was intended to apply the method used by Elliot Smith in his study of the Egyptian brain where he was able to utilise the variations in the thickness of the cortex and the changes of cortical bands to define such areas. I found, however, that these formalin-fixed brains did not disclose with sufficient sharpness these differences, and no significant facts were obtained outside the visual area. There can be no doubt, however, that it would be a distinct advance in anthropological method if the pattern of the cortex were elucidated and compared by his method.

SOURCE OF THE MATERIAL

Brain 1 was obtained from the Mental Hospital and belonged to a full-blooded aborigine from Welgena. The cause of death was congestion of the lungs and cardiac failure. He was 5 feet 5 inches in height and was 56 years of age. The brain was fixed *in situ* and the preservation was excellent.

Brain 2 was also obtained from the Mental Hospital and belonged to a full-blooded aborigine from Horse Shoe Bend in the Northern Territory of Australia. This man was 5 feet 8 inches high, was 24 years of age, and died of pulmonary tuberculosis. The brain was fixed *in situ* and the preservation was excellent.

Brain 3 came from a general hospital. His age was 36, but no other details of his physique are known. The cause of death was heart failure with some cirrhosis of the liver. The preservation was excellent.

Brain 4 was badly preserved and distorted and could only be used for one or two points in the following description.

The fact that two of the brains came from the asylum is, I believe, without any significance in the results which follow.

THE FISSURATION OF THE BRAIN

Exposure of the Insula

Using Brain 1 as a sort of standard, it is noted that exposure of the insula occurs in both hemispheres. In Brain 2 the exposure is marked in the left hemisphere but absent in the right. In Brain 3 the insula is covered in both hemispheres. Brain 4 is useless for comparison because of bad fixation and distortion. Duckworth's material created difficulties, since he was unable to discount distortion from imperfect fixation, the effects of removing the vessels and membranes, and what was due to defective operculation. Nevertheless he was inclined to regard exposure of the insula as a character of the aboriginal brain and as being due to defective development of the orbital operculum. I believe it is in a slight degree a feature of the aboriginal brain, for in well-fixed material it is possible to get rid of all the difficulties except those of the range of variation and dolichocephaly. From the comparisons that can be made with brains available here of dolichocephalic type its importance as a feature

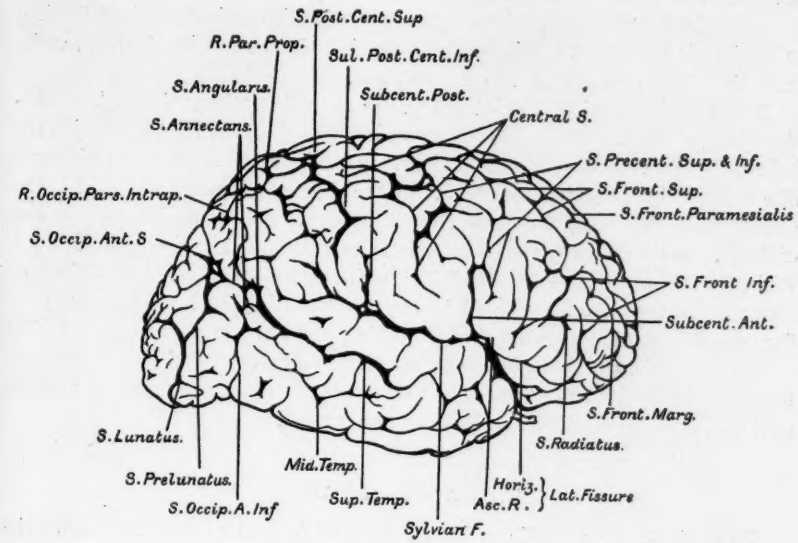

Fig. 1. Brain 1. Right hemisphere. Lateral view.

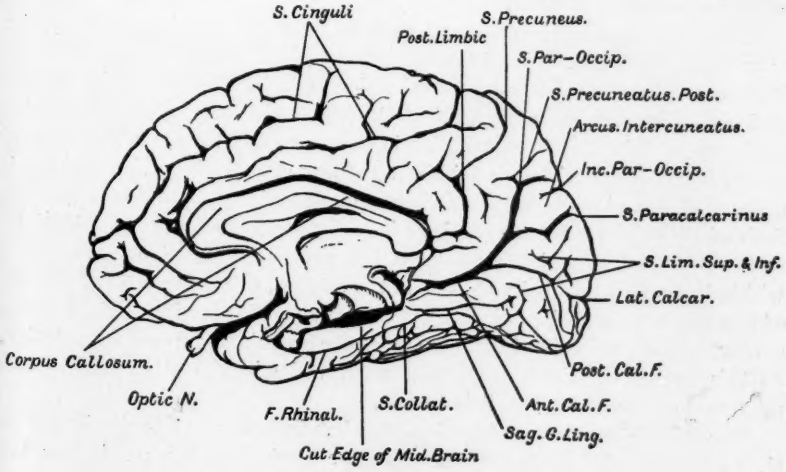

Fig. 2. Brain 1. Right hemisphere. Mesial view.

of the aboriginal brain seems enhanced since it appears that the insula is covered even in the most dolichocephalic examples of European brains.

In Brain 1 the fronto-parietal operculum of both hemispheres is defective, in Brain 2 it is present but imperfect, especially in the left hemisphere, while in Brain 3 it is well developed on both sides.

The anterior rami of the lateral fissure are extremely variable. The outstanding point seems to be the close proximity of the ascending limb with the inferior portion of the precentral sulcus. In Brain 3, the arrangement is more like the usual textbook illustration. In the right hemisphere of Brain 1, the ascending limb does not emerge from the fossa. It is tempting to try, but difficult, to establish any significance in the arrangement of these rami. Much variation has been recorded in all the brains examined. The observations of other observers have been tabulated by Duckworth. The lateral fissure calls for no particular comment. There is nothing peculiar to note in regard to the sulcus circularis, the limen insulae, the central sulcus, the gyri breves or gyrus longus, except that in one case the breves are arranged as a series of parallel gyri equal to one another and to the gyrus longus.

THE ACOUSTIC AREA

In Brain 1, the acoustic gyri are separated from the lateral surface of the superior temporal convolution by a deep indentation. In Brain 2 the posterior transverse gyrus is large and prominent in the right hemisphere. The acoustic area however passes on to the lateral surface without interruption. The same extension occurs in Brain 3.

The area circumambiens can be defined by the middle portion of the superior temporal convolution. This middle component of the superior temporal sulcus is separable from the anterior and posterior parts by the presence of sunken gyri within the fissure. In two hemispheres (1, left and 2, right) the interruption of the superior temporal convolution is complete, and the superior temporal convolution unites with the middle temporal convolution. This feature is perhaps of some significance in a dolichocephalic brain. The posterior ascending limb of the superior temporal sulcus is easily separable from the middle by means of a gyrus which may be either superficial or slightly depressed within the sulcus but easily seen from the surface, or sunken so that the lips of the sulcus have to be pulled apart in order to discover it. Brain 3 shows a very marked reduction in the width of the superior temporal convolution. In this brain the width drops to 9 mm., while in the other hemispheres measured at the same spot, it is 15 mm.

The middle temporal sulcus is somewhat irregular but probably less so than in other dolichocephalic brains. In one hemisphere it is continuous, but in the others it occurs in two parts, an anterior and posterior.

The inferior temporal sulcus is variable. In the right hemisphere of Brain 1, it forms a continuous sulcus running parallel with the collateral fissure. The

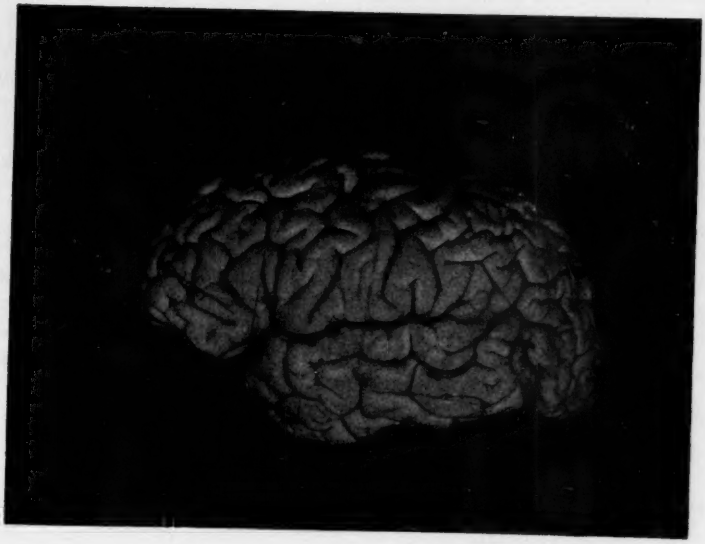

Fig. 3. Brain 1. Left hemisphere. Lateral view.

Fig. 4. Brain 1. Left hemisphere. Mesial view.

same arrangement also occurs in the left hemisphere. In both it travels medially around the front end of the collateral, either ending near to or joining with the rhinal fissure. In Brain 2, left hemisphere, it forms a continuous fissure. At its middle it is joined by the collateral fissure. On the right side in Brain 2 the condition is practically the same, except that it is not actually joined by the collateral. In Brain 3, the fissure is broken up into at least three parts in both hemispheres.

In Brain 1 the pararhinal area is very much reduced in size by the encroachment of the superior temporal sulcus. In Brain 2 the pararhinal area is well defined. In Brain 3 it is again much reduced in size.

The temporal area as a whole appears to be small. In the simplest brain the sulci tend to be continuous fissures, except in the case of the superior temporal fissure in which the components tend to remain separate. In the same brain the auditory receptive area is better demarcated from the lateral surface than in the others. On the whole it does not seem possible to assign any distinctive features to the acoustic area of the Australian brain.

VISUAL AREA

The calcarine fissure falls into three portions—anterior, posterior, and lateral (superior occipital sulcus of Duckworth and others). In only one hemisphere (the right of Brain 3) is a typical sulcus lunatus absent.

The interval between the posterior calcarine and the lateral calcarine is marked by the presence of vertical gyri. These may be elevated, depressed, or at the same level as the surrounding cortex. There may be one, two, or three of them. They are least conspicuous in the left hemisphere of Brain 1. The limiting sulci are easily identified and the sulcus sagittalis lingualis is present in all. The sulcus parieto-occipitalis (sulcus precuneus of Duckworth) is followed in all hemispheres by an exposed arcus intercuneatus which is cut at the superomesial border of the hemisphere by the incisura parieto-occipitalis. This is followed by a sulcus paracalcarinus which is usually continued on to the lateral border as the lateral superior occipital sulcus.

The lateral calcarine sulcus, beginning as a V-shaped fissure, turns round the occipital pole and ends on the lateral occipital surface without bifurcation. Beyond this lies the curved lunate sulcus which can be identified without doubt in all brains except the right hemisphere of 3. From the middle of the lunate the sulcus prelunatus extends forwards along the lateral surface terminating anteriorly in the anterior occipital sulcus. This is joined by an annectant fissure to the angular sulcus which is coincident usually with the superior temporal fissure. In Brain 1, right hemisphere, a distinction can be made between the terminal ascending limb of the superior temporal sulcus and the sulcus angularis.

This pattern can be made out most easily in the two hemispheres of Brain 1. The same pattern exists in the remaining hemispheres, but the arrangement

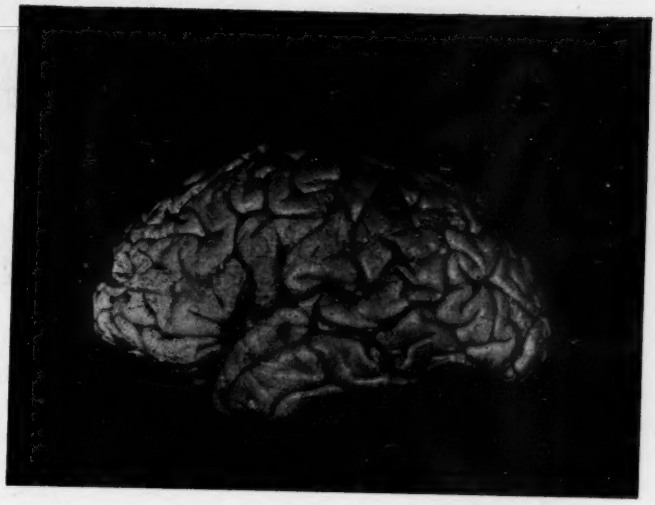

Fig. 5. Brain 2. Left hemisphere. Lateral view.

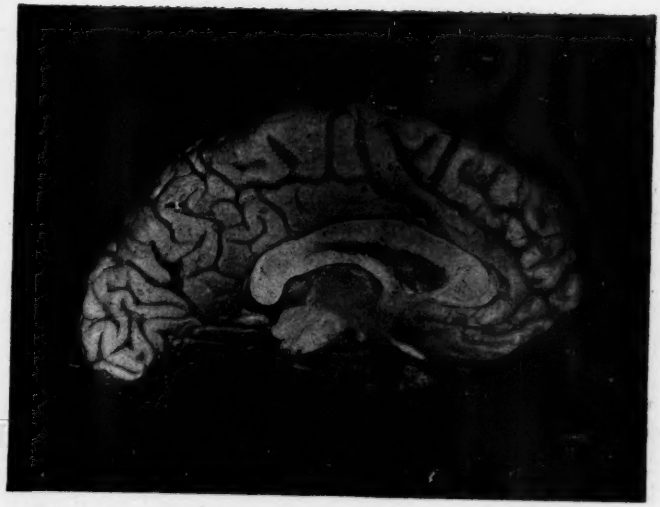

Fig. 6. Brain 2. Left hemisphere. Mesial view.

is not so clear. The detailed differences do not appear to be of any moment since the variation is in no two cases the same.

As some importance has been attached to the depth of the fissures, a few comparative measurements are included here:

Brain No.	Hemisphere	S. par.-occip. (mm.)	S. calcar. (mm.)	S. centralis (mm.)
1	R.	17	15	18
	L.	16	15	18
2	R.	22	15	22
	L.	19	18	20
3	R.	20	20	20
	L.	15	19	17

The only inference that can be drawn from these figures perhaps is that in Brain 1, where the visual area has achieved a more marked external definition, the calcarine fissure tends to be shallower.

When compared with European brains the significance of the frequency of the lunate sulcus is apparent. Duckworth computed when he wrote that 60 per cent. of all aboriginal brains, so far described, possessed a lunate sulcus. The addition to his series of the above would raise that percentage still further (seven out of eight hemispheres examined). The significance and meaning of this sulcus was first deciphered by Elliot Smith. Examination of the cortex in these cases confirms his interpretation. It is the one certain primitive feature yet discerned in the human brain. The presence of the paracalcarine sulcus seems very constant and this may be of some significance in emphasising the primitive character of this region of the brain. There is one other feature which perhaps is worth recording, and that is the tendency towards operculation that occurs at the extremity of the inferior arm of the anterior occipital sulcus. The operculum separates the peristriate area from the occipito-temporal area and is especially marked in Brain 1. It is very obvious in the left hemisphere of this brain.

The sulcus collateralis does not join the rhinal fissure in the left hemisphere of Brain 1. In the right these two are connected only superficially, while near this junction a lateral prolongation of the collateral occurs which separates the pararhinal from the temporal areas. Posteriorly it terminates in a transverse expansion bounding the peristriate area. In Brain 2 this fissure joins the inferior temporal sulcus. In the left hemisphere of Brain 3 it joins with the rhinal fissure anteriorly.

THE PARIETAL AREA

A tendency for the sulcus centralis to join the Sylvian fissure has been raised to the rank of a distinctive attribute of the Australian brain. Duckworth however in his series failed to confirm this. In the right hemisphere of Brain 1 there are extremely indirect communications with the Sylvian by way of the sulcus subcentralis anterior, and still less so by way of the sulcus

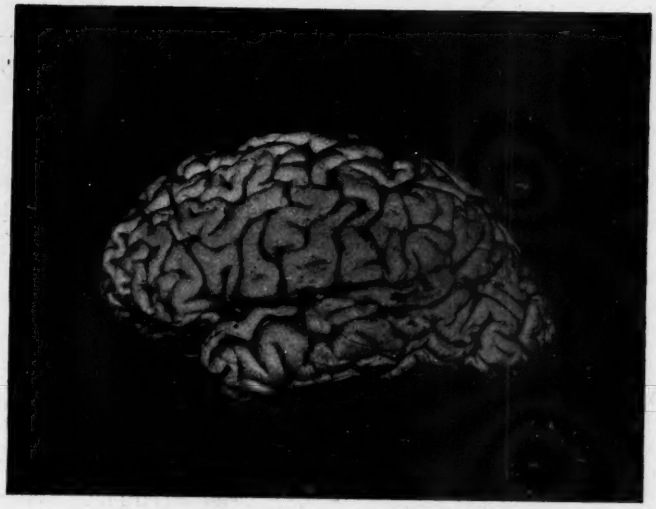

Fig. 7. Brain 3. Left hemisphere. Lateral view.

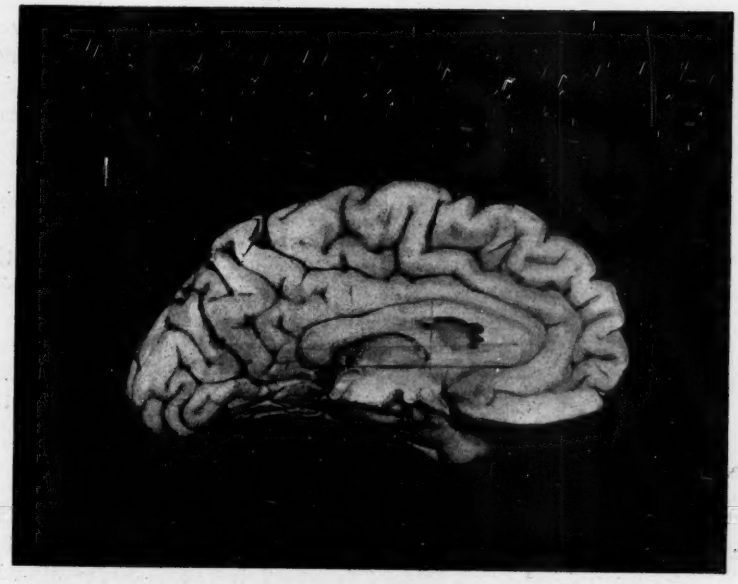

Fig. 8. Brain 3. Left hemisphere. Mesial view.

subcentralis posterior. In the left hemisphere there is no indication of any continuity, even indirectly.

In Brain 2 in the right hemisphere there is no communication with the Sylvian fissure. On the left side, however, the central sulcus is joined by the sulcus subcentralis anterior and is thus brought into communication with the Sylvian fissure.

In Brain 3 no such communication exists on the right side, but on the left side the central sulcus is again joined by the sulcus subcentralis anterior, thus establishing communication with the Sylvian. In the very imperfect Brain 4, the sulcus centralis is excluded from the Sylvian fissure.

Duckworth found such communication present in only one of his hemispheres, while in half of the cases of the well-preserved brains in this series it is present. The feature is thus perhaps of some importance.

Another point that is of some interest is the relation of the fissure to the superomesial border. In all cases there is a well-defined continuation of the fissure to the superomesial border and in some cases beyond. There seems to be no substantial difference in the arrangement from that of other brains. By the examination of unstained cortical strips no evidence was obtained of extension forwards of the Rolandic area. A well-defined lobus paracentralis limited behind by the sulcus cinguli and in front by the sulcus paracentralia is present.

The sulcus intraparietalis consists of four genetically distinct furrows. Duckworth observed that in 47 per cent. of his cases the occipital element did not fuse with the intraparietal. In this series all four elements are continuous though the fissure can easily be split up into its components by the presence of annectant gyri slightly depressed below the surface of the brain. The point that impresses one is the nearness of the fissure to the superomesial border so that the superior parietal lobule is reduced to the smallest proportions. The reduction is marked in Brains 1 and 2, while in 3 the width is normal.

The cuneus is defined by the sulcus precuneus, the terminal ascending piece of the sulcus cinguli, and inferiorly by a sulcus paracentralis.

The gyri supramarginalis and angularis are difficult to define owing to the lack of regularity in the fissures of this region. The sulcus angularis joins with the superior temporal sulcus below and usually directly or indirectly links up with the intra-parietal above. Duckworth believes the parietal area is small relatively. The tendency for the intraparietal sulcus to approach the superomesial border tends to enlarge the area occupied by the supramarginal and the angular gyri.

FRONTAL REGION

The inferior limb of the precentral sulcus is confluent with the superior portion in only two hemispheres out of six. This is much less than in Duckworth's series (62·5 per cent.) and thus brings this series into greater conformity with the European brain. Below, in the right hemisphere of Brain 1, the inferior

precentral is joined to the Sylvian fossa by the anterior subcentral fissure. In the left hemisphere the sulcus subcentralis anterior is present, but the inferior precentral is joined to the Sylvian fossa by means of the sulcus diagonalis. In Brain 2 on the right the junction with the Sylvian fossa by means of the anterior subcentral is just discernible, while on the left side the fissure is directly continuous with the fossa.

In Brain 3 both inferior precentral sulci approach and are only narrowly excluded from the fossa by a small depressed gyrus. The junction with the fossa appears to be a variable feature in the European brain and perhaps the frequency of this union is slightly higher in the Australian brain. The sulcus subcentralis anterior is present in four hemispheres, about the same proportion as Duckworth found. The sulcus radiatus of Eberstaller is present in all cases. This makes the brain like that of the European foetus (Duckworth).

A fronto-marginal sulcus and sulci rostrales can be distinguished in all brains, thus making the Australian brain resemble the European brain.

In all cases the superior frontal sulcus is continued almost to the frontal pole and is directly continuous with the superior precentral sulcus. In only one hemisphere (Brain 3, right hemisphere) is the sulcus precentralis medius independent of the superior precentral sulcus. Duckworth also found one hemisphere in which this occurred and believed it to be a Simian feature.

A sulcus frontalis medius is present in all. Usually well defined and separate at its posterior extremity, anteriorly it becomes very irregular and fuses with the fronto-marginal sulcus. The tendency of this fissure to become an independent sulcus is noted by Duckworth and regarded by him as a very distinctive feature of the aboriginal brain. This series confirms in part the data of Duckworth, though in only two hemispheres can it be said to be distinct from the fronto-marginal sulcus, a very much smaller proportion than in his series.

In all hemispheres the superior frontal gyrus is divided by a longitudinal furrow more or less regular, running parallel with the superior frontal sulcus. A similar furrow is present on the mesial aspect of the brain. Both are present in Brains 1 and 2, while in Brain 3 the lateral paramesial fissure is present on the left side and a medial paramesial on the right side.

The sulcus cinguli is present with the same form in all.

The excellent and intensive study of the aboriginal brain made by Duckworth has facilitated enormously the work of anyone who undertakes a similar study. Full use of his paper has been made by me, and it would perhaps be suitable at this point to see what agreement the present study gives in regard to the fissuration when compared with his.

(1) Curvature of the fissure rhinalis. A boldly curved fissure rhinalis is evidence of lowly affinities, says Duckworth. This character Duckworth found once. This feature occurs in Brain 1, the simplest of the series. It is not present in the others.

(2) Exposure of the insula. The evidence for this has been discussed above. The present series being excellently preserved removes the doubt felt by

Duckworth on this point, and exposure of the insula is to some extent a distinctive feature of the aboriginal brain.

(3) Discontinuity of the components of the sulcus intraparietalis impressed Duckworth with the primitive quality of the aboriginal brain, particularly the separation of the superior postcentral from the parietalis propius. The present series does not confirm this opinion, for in all the sulcus is continuous throughout.

(4) In regard to the retrocalcarine fissure and the sulcus lunatus, the present series amply confirms, and even carries further, the inferences to be drawn from this feature. In the identification of these fissures Elliot Smith has discovered so far the only reliable criterion of a primitive human brain. The present series indicates that these features are present practically in all pure-blooded aborigines.

(5) The gyrus cuneus and the annectant gyri are as Duckworth states.

ANTHROPOMETRY

In this part of the study of the aboriginal brain the recent work of Kappers has been followed. Kappers has insisted on the absolute necessity of using only properly preserved material, and has drawn up a series of measurements which have the merit of simplicity and at the same time the virtue of expressing all the information desired. Kappers' series of dolichocephalic Dutch brains furnish an excellent basis for comparison with the Australian brain.

Taking first the brain index, i.e. the figure derived from the greatest diameter of the brain over its greatest length, in Kappers' series of seven Dutch brains this index ranges from 75·2 to 80·3; in this series of well-preserved brains the indices are:

Brain	Greatest diam. (mm.)	Greatest length (mm.)	Brain index
1	126	173	72·83
2	124	173	71·68
3	128	170	75·30

This then is a degree of dolichocephaly very much greater than that in the brains chosen by Kappers.

The height index is obtained by taking the height of the parietal perpendicular from the lateral horizontal plane, i.e. a horizontal plane connecting the orbital operculum with the base of the occipital lobe. This index is of interest in the Australian because of the marked flattening of the vertex of the skull in many of them, and this causes what has been described as the ill-filled cranium of the Aborigine.

Following the suggestion of Kappers, these measurements have been obtained from photographs, a much more accurate method than measuring them on the actual brains. The results are:

Brain	R.	L.
1	0·521	0·502
2	0·500	0·522
3	0·481	0·477

The average works out for the height index at 0·5. In Kappers' series of dolichocephalic Dutch brains the average for the height index is 0·491. Thus the two are in practical agreement. The relationship of height to length is thus in the same proportion as in dolichocephalic brains generally, and there is no reason to suppose that the Australian cranium is an ill-filled one. Duckworth writes, "As compared with European crania, that of the aboriginal Australian appears to be incompletely expanded and this is ascribed to defective growth of the cerebrum." The series considered by Duckworth failed, however, to confirm the above quotation. This, he thought, was due to their lack of adequate preservation.

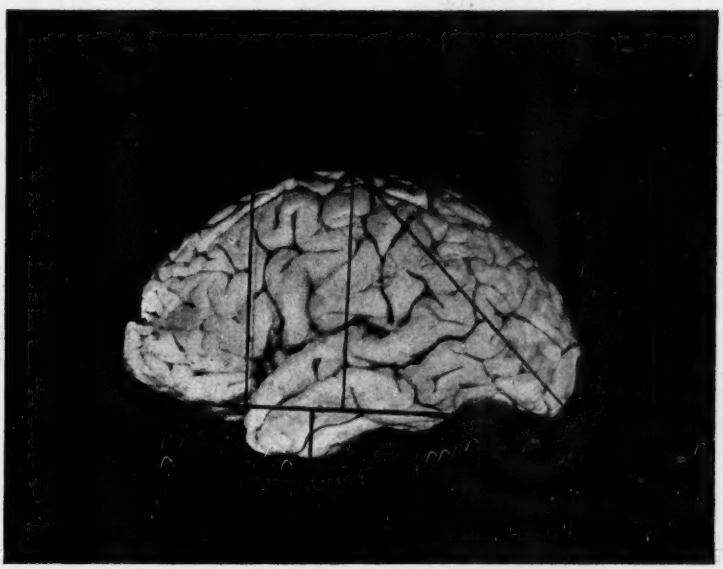

Fig. 9. The lines indicate the measurements which have been used in the anthropometry of aboriginal brain.

The occipital index being the parietal perpendicular divided by its distance from the occipital perpendicular, is subject to some fluctuation, for the highest point of the parietal lobe may cause a considerable shift in the position of the parietal perpendicular. In this series the line of the parietal height lies more anteriorly than the illustration of Kappers shows. This shift is particularly true of Brain 3. The other two give almost identical figures with those of the Dutch dolichocephalics. These average 1·19. The average for two brains of the present series is 1·09, while the third falls to 0·8, this being due to the anterior position of the parietal perpendicular. When the distance to the occipital perpendicular is measured from a constant point, namely, the point where

the central sulcus cuts the superomesial border, the index of Brain 3 rises to 1·0. It has already been seen that the ratio of the parietal height to the lateral horizontal is the same in the Dutch and Australian brains. When this same height is compared with the distance from the occipital pole the index is diminished. This diminution in the value of the index may arise from the increase in the distance to the occipital perpendicular, and may be explained by the increase in the area of the visual territory.

The temporal index is obtained by dividing the temporal perpendicular by the lateral horizontal distance. The indices vary, but the average is 0·127. Kappers' series gives an average of 0·145. Therefore the temporal area may be relatively reduced in the aboriginal brain.

The frontal height index is obtained by dividing the perpendicular from the lateral horizontal to the upper border through the front of the temporal pole (measured from the lateral horizontal) by the lateral horizontal. The average for the Australian is 1·728. The average for the Kappers' series is 1·85. This again indicates a reduction in the Australian brain.

The frontal length index is the distance of the insular perpendicular from the frontal pole perpendicular divided by the lateral horizontal. The Australian average is 0·254. The Kappers' series averages 0·231. The higher value of the Australian indicates that there may be a greater extension in the frontal region.

It appears from all these measurements that those which depend on vertical measurements are decreased in the Australian, while those depending on horizontal measurements are increased. It may therefore be concluded that in the Australian brain the relative magnitudes of the brain are much the same as in the European brain. What differences are present depend entirely on the greater dolichocephaly of the Australian brain.

The callosal height, being the callosal perpendicular divided by the callosal length, is for the Australian brain 0·310, while for the Kappers' series it is 0·321. This slight difference is again readily explained by the greater dolichocephaly of the Australian brain. The pre-callosal and post-callosal lengths may be similarly expressed as indices in terms of the total brain length. Duckworth has used a similar comparison. His figures show considerable individual variation. The pre-callosal index in three cases is between 18 and 19, while in one case it is 13·6. The present series is quite self-consistent and gives an average value of 20·24, somewhat higher than Duckworth's values. The values for the Kappers' series I have calculated from his chart, and the average value is 18·5. The post-callosal index for the Australian in my series is 33·78. For Duckworth's series, three hemispheres are 33. For a Dutch dolichocephalic the average is about 30. Again we are dealing with an expression of the extreme dolichocephaly of the Australian brain.

Thus from a comparison of the indices we arrive at the general conclusion that the variations in the indices of the Australian brain present no peculiar features, and the differences that exist between it and the European dolicho-

cephalic brain are all understandable in terms of the greater dolichocephaly of the Australian.

Table of Indices of Aboriginal Brains.

Origin of brain	L.B. index brain	Height index	Occipital index	Temporal index	Frontal height index	Frontal length index	Callosum height	Stem angle
Full-blood Aborigine								
(1) R. hemisphere	72·83	0·521	1·123	0·128	1·878	0·235	0·319	108°
L. hemisphere	—	0·510	1·014	0·134	1·852	0·241	0·319	—
(2) R. hemisphere	71·68	0·500	1·093	0·107	1·742	0·250	0·352	107°
L. hemisphere	—	0·522	1·142	0·110	1·702	0·272	0·333	—
(3) R. hemisphere	75·3	0·481	0·846	0·152	1·552	0·277	0·267	105°
L. hemisphere	—	0·477	0·833	0·132	1·617	0·250	0·271	—
Average	73·27	0·502	1·008	0·127	1·728	0·254	0·310	106·6°

	Precallosal index	Postcallosal index
(1)	L. = 20·56	L. = 32·6
	R. = 19·3	R. = 33·14
(2)	L. = 20·6	L. = 36·0
	R. = 20·0	R. = 32·14
(3)	L. = 22·03	L. = 33·8
	R. = 19·0	R. = 35·0

PERCENTAGE OF GREY MATTER PER HEMISPHERE

The final investigations made on these Australian brains concerned themselves with the relative proportions of the grey and white matter per hemisphere, and to the brain as a whole. For this purpose we used the method introduced by Kappers. In his paper there is a discussion of the various methods that have been used for this purpose. At first I was disposed to believe that the method would only give a poor approximation to the real values, but after trying it out I was persuaded that even when different people carried out the necessary manipulations the degree of agreement between the results suggested that the method was sufficiently valuable to be applied to these brains.

The brain was hardened in 10 per cent. formalin and weighed. The cerebellum was then removed and the hemispheres divided in the sagittal plane, and the parts weighed. By means of Reichert's macrotome the hemispheres were cut in 2 mm. sections, and then by means of a mounted safety razor blade the cortex was separated from the rest of the hemisphere. The separation was made easy by first staining the cortex with 1 in 1000 nigrosine for 3 hours. Since the moisture absorbed by the brain when cut into many small pieces is greater than that contained originally in the brain, drying must be allowed to proceed until the final weight of the cortex and white matter is the same as that of the undivided hemispheres. There is probably an exaggeration of the amount of cortex present, for in cutting the cortex from the white matter there is a tendency to preserve the cortex at the expense of the white matter.

The results are as follows:

Right Hemispheres.

Brain	Total brain weight (gm.)	Weight of hemisph. (gm.)	Weight of cortex (gm.)	Weight of white matter (gm.)	% cort. per hem.	% cort. total br. wt.
1	1138·0	481·5	224·7	256·8	46·66	19·74
2	1123·0	495·0	240·0	256·0	48·5	21·04
3	1044·6	442·1	242·1	200·0	54·76	21·26

Left Hemispheres.

1	1138·0	482·5	240·0	242·5	49·74	21·23
2	1123·9	481·0	227·5	253·0	47·36	20·2
3	1044·6	448·0	238·0	210·0	53·2	22·8

The average of the cortical percentage per hemisphere in all the specimens is 50·04 per cent. This might be compared with that found by Kappers for the Dutch brains 50·65 per cent., and for Chinese brains 50·45 per cent. The slight differences present may well be explained by the errors of the method. Thus it is concluded that the ratio of white and grey matter in the aboriginal brain is in the same proportion as in other human brains. The percentage weight of the grey matter to the total brain weight is also in close agreement with the figures supplied by Kappers.

The only other point that impresses one in these figures is the lowness of the value of the weight of the whole brain and the weight of each hemisphere. The highest brain weight is obtained in Brain 1, which on other grounds was considered the simplest of the three. Though the brain weights given here can be matched easily among European brains, yet it is to be observed that three random aboriginal brains gave an average total brain weight of 1095 gm., and the brains tabled by Kappers contain one of the same order as the aboriginal brains, while the others are much higher, the average being nearly 1268, a difference of 150 gm. Thus, by the method employed, no significant difference is disclosed in the amount of white matter and grey matter in the Australian brain from that found in other races.

A comparison of the hemispheres of the two sides reveals no constant difference between them. Sometimes the left and sometimes the right has the higher percentage of grey matter. This again is in agreement with the results obtained by Kappers.

The general result of this enquiry, employing a comparison of fissural pattern, of anthropological indices, and finally the ratio of cortex per hemisphere, is to bring the Australian brain into agreement with other human brains. These observations offer no ground for supposing that the aboriginal brain discloses any peculiar simian features, or that it resembles microcephalic brains of European origin, or that it retains any special features of the foetal human brain. Anthropological differences reside in the extreme dolichocephaly of the aboriginal brain. The distinguishing features of the Australian brain are the presence of the following characters together: it is a small brain; it is

extremely dolichocephalic, the insula tends to be exposed, and it retains primitive features in the organisation of the striate area. No other characters have been disclosed by this enquiry.

SUMMARY

1. The fissural pattern of the aboriginal brain shows two features which distinguish it from European brains in general: (*a*) the retention of a paracalcarine fissure and a sulcus lunatus; (*b*) a tendency for the insula to be exposed. The general disposition of the remaining fissures and their variations are best accounted for by the extreme dolichocephaly of the brain.

2. Variations from the measurements of European brains are adequately accounted for by the extreme dolichocephaly. The proportions of the various regions of the brain are of the same order as in European brains.

3. The proportion of grey matter per hemisphere is the same as in European brains.

4. The total brain weight and also the weight of the hemispheres appear to be smaller than in European brains.

5. There are no significant differences between the right and left hemispheres.

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THE TASMANIAN SKULL

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The present paper is intended to be the first of a series designed to furnish fellow anthropologists with what may be termed graphic reproductions of the average or composite skulls of various racial types. So great a number of pages of our journals have been filled by column after column of figures recorded upon measured series of crania that it may be justifiable to reproduce these typical average normae of racial types from which any one may gain an idea of the general form of the skull and, at the same time, derive the average measurement of any details he may wish to determine.

No description of the figures is necessary, since the type contours depict all the features of the four normae; but certain minor, but not unimportant, details such as are not shown in the figures are described; no measurements are appended, since they may be taken confidently from the contours.

In dealing with the Tasmanian I have not ventured to determine the sex of the skulls and both sexes are, therefore, included in the composite. This decision is the result of experience in dealing with the skulls of Tasmanians and Australians. It would have been easy to have sorted the drawings into two groups; those that looked like what we consider male Tasmanian skulls should be, and those that conform to our standards of the female: but I see no utility in this proceeding, since the opportunities for checking our determinations by reference to the rest of the bones of the skeleton or with the known history of the individuals are so few. Had I sexed the skulls and produced two type contours I have no doubt that one would have conformed to our ideas of masculinity and the other have had female characteristics: but I doubt if this would have added any value to the investigation.

MATERIAL

The excellent dioptographic drawings published by Berry (1) were used as the basis of this work, and dioptographic drawings and notes made upon six additional skulls (2) were also made use of. Advantage has also been taken of Hrdlička's recently published results (3) and the principal papers and books dealing with the Tasmanian skull have been consulted.

METHOD

On the drawing of the norma lateralis the Frankfurt plane is ruled and the central point of the upper border of the external auditory meatus (meatal

point) is taken as the measuring point. From this point lines are ruled to the chief anatomical landmarks (nasion, glabella, bregma, lambda, inion, mastoid, maxillary point, alveolar point and spinal point), and the angles that these lines make with the Frankfurt plane are determined. In addition to these radii, lines are ruled at 10-degree intervals cutting the periphery of the skull in a complete circle from the meatal point as a centre and with the Frankfurt plane as the horizontal axis (see fig. 1). Forty-five radii are, therefore, ruled upon each drawing and each of these radii cuts several anatomical landmarks, such as suture lines, etc., in its passage from the centre to the periphery. The distance of each such point is measured from the meatal point along each of the forty-five radii. With the norma facialis the Frankfurt plane is ruled and its central point is taken as the measuring point, the angles of the main anatomical landmarks being determined as before and the thirty-six radii ruled (see fig. 2). With the norma occipitalis the Frankfurt plane is determined by superimposing the drawing reversed upon the drawing of the norma facialis, the mid-point is determined by the same method and the same procedure adopted (see fig. 3). In the case of the norma verticalis, the relation of the bregma and the lambda to the mid-sagittal plane are already determined: this mid-line is ruled. From the norma lateralis the position of the bregma in relation to the meatal point is known, and the inter-meatal plane is taken as the transverse axis from which the radii are drawn (see fig. 4).

By this method it is claimed that the radii are sufficiently numerous and the intervals between them sufficiently small to obtain a precise recording of all the contours of the skull, and in addition the principal landmarks are definitely localised in relation to a precise measuring point and to a fixed plane.

When all the radii on all the drawings have been drawn, all the measurements are taken and recorded. The average is then determined for each individual measurement. The method is somewhat laborious. Upon the drawings of the four normae, 480 points are measured and their measurements recorded on the average skull. This means that in the making of a reconstruction from a series of only 50 skulls (as in the present investigation) 24,000 measurements are available for mathematical treatment. In the case of the anatomical landmarks, the average angle at which the point lies in regard to the fixed plane is determined and then the average distance of the point from the fixed measuring point is calculated. In the case of the radii of fixed angle, the average distance of each anatomical feature intersected by the radius is determined from the fixed point. When all the averages have been worked out, the radii are redrawn, the average distances of the anatomical features from the measuring point are marked off and the average outline for that norma may be reconstructed. Although the method is laborious it is claimed for it that it ensures a considerable degree of accuracy in depicting the average skull of any racial series. More is hoped from it; for it is possible that when a number of racial series have been graphically reconstructed, we may be in

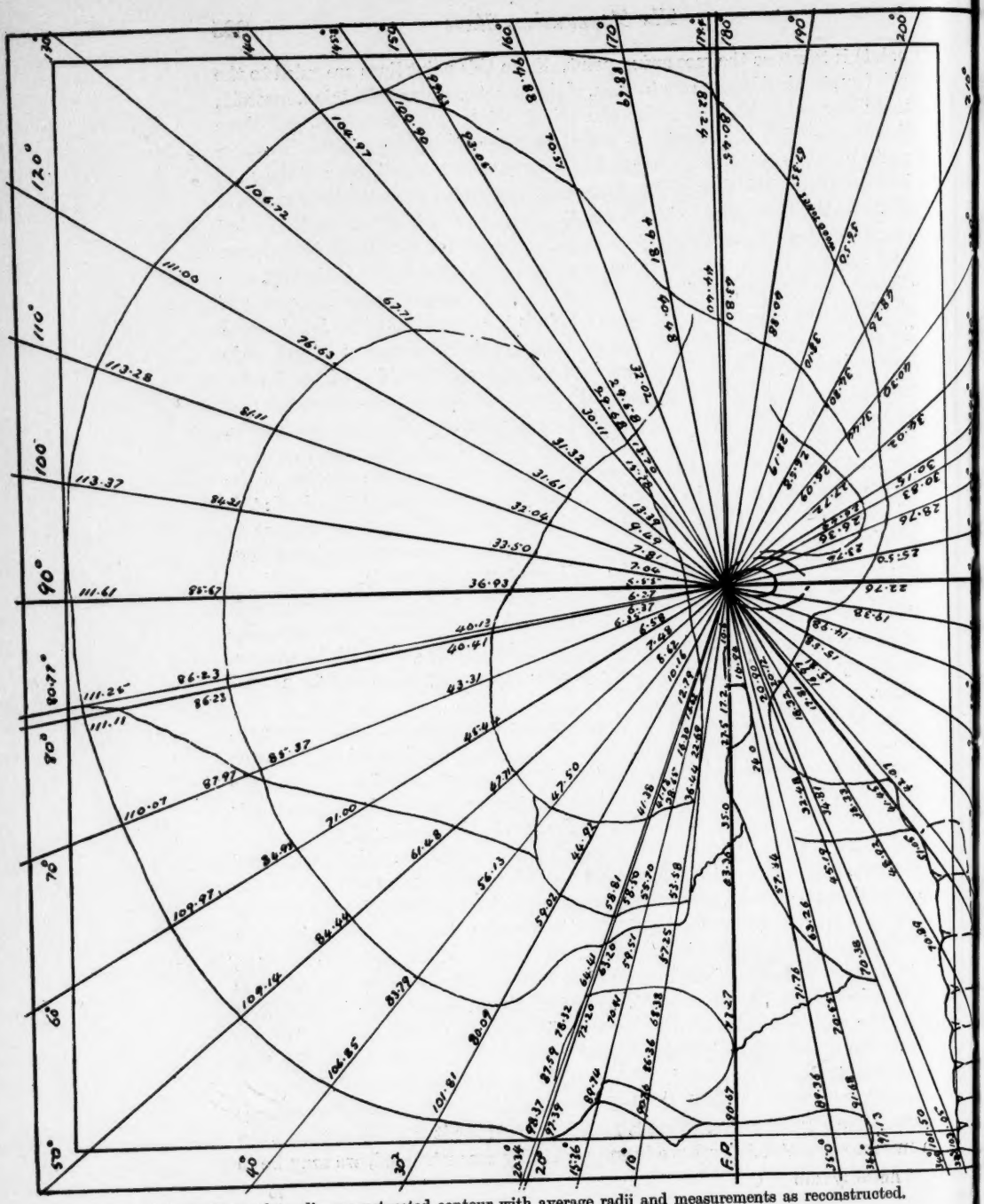

Fig. 1. Norma lateralis, reconstructed contour with average radii and measurements as reconstructed.

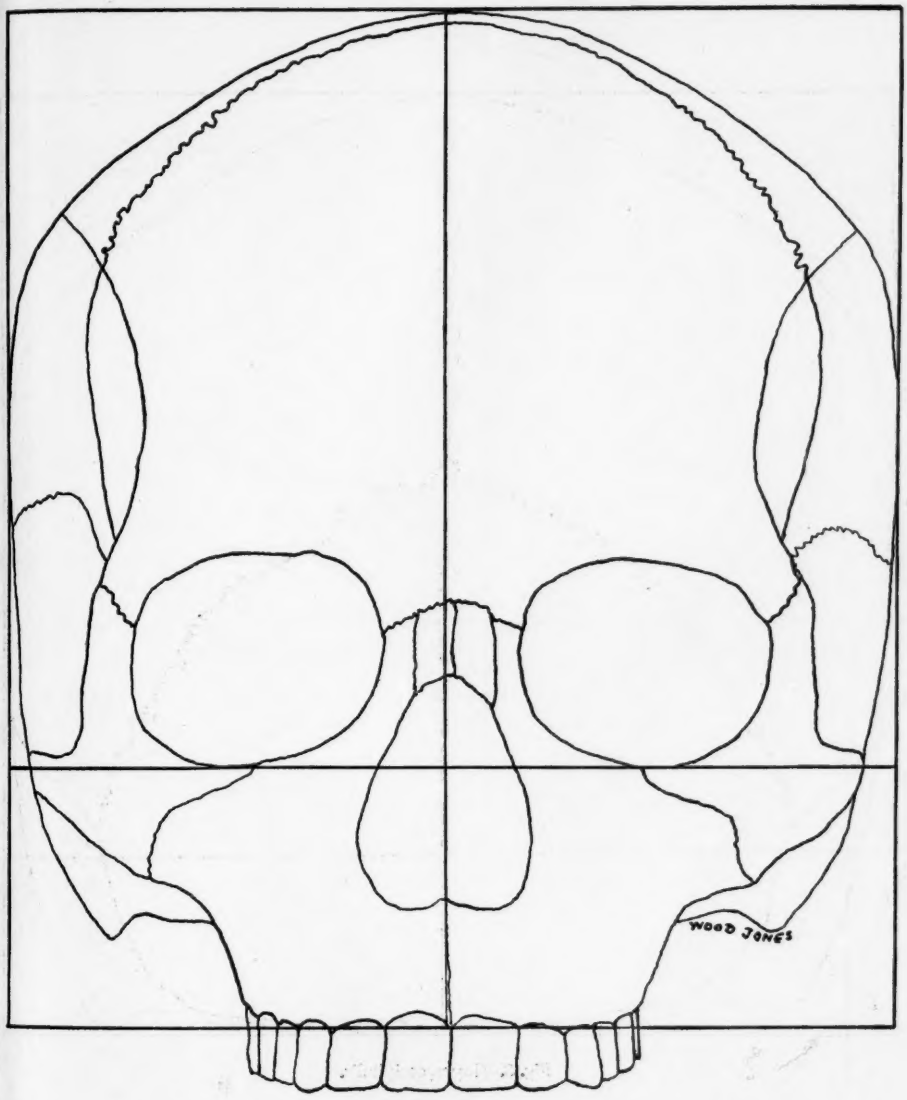

Fig. 2. Norma facialis. (In this and the following two figures the radii and measurements have been omitted.)

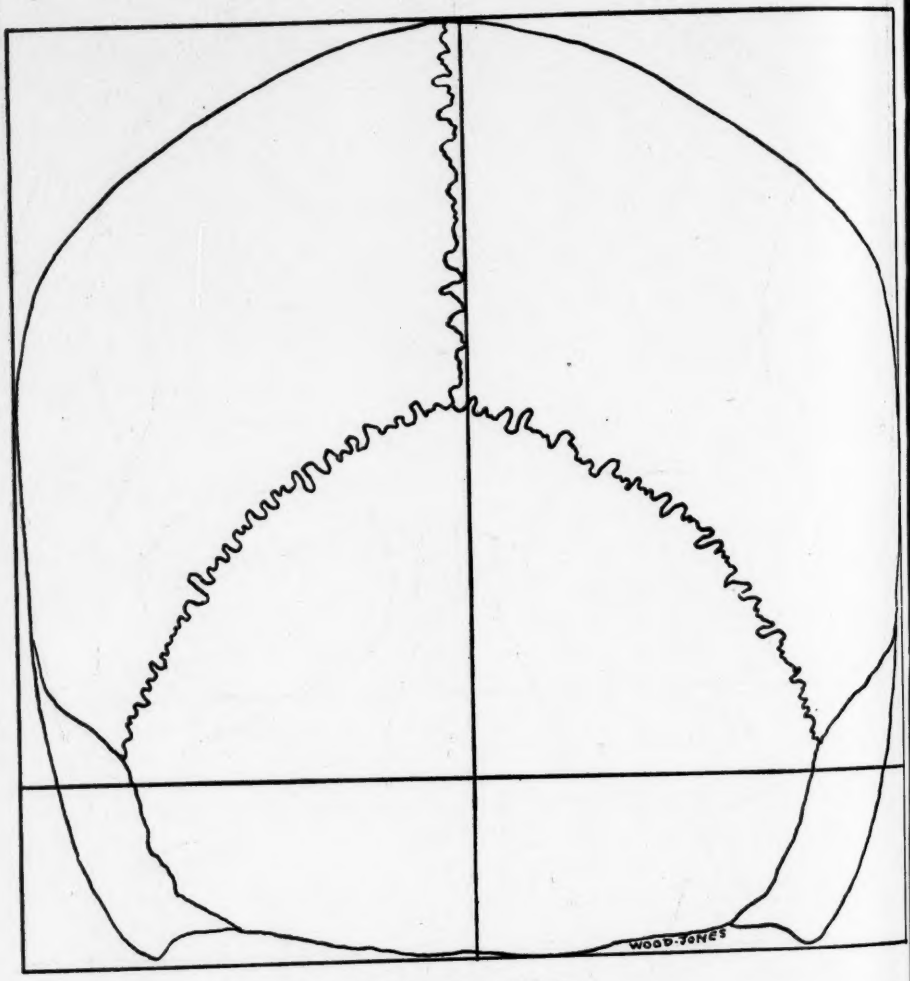

Fig. 3. Norma occipitalis.

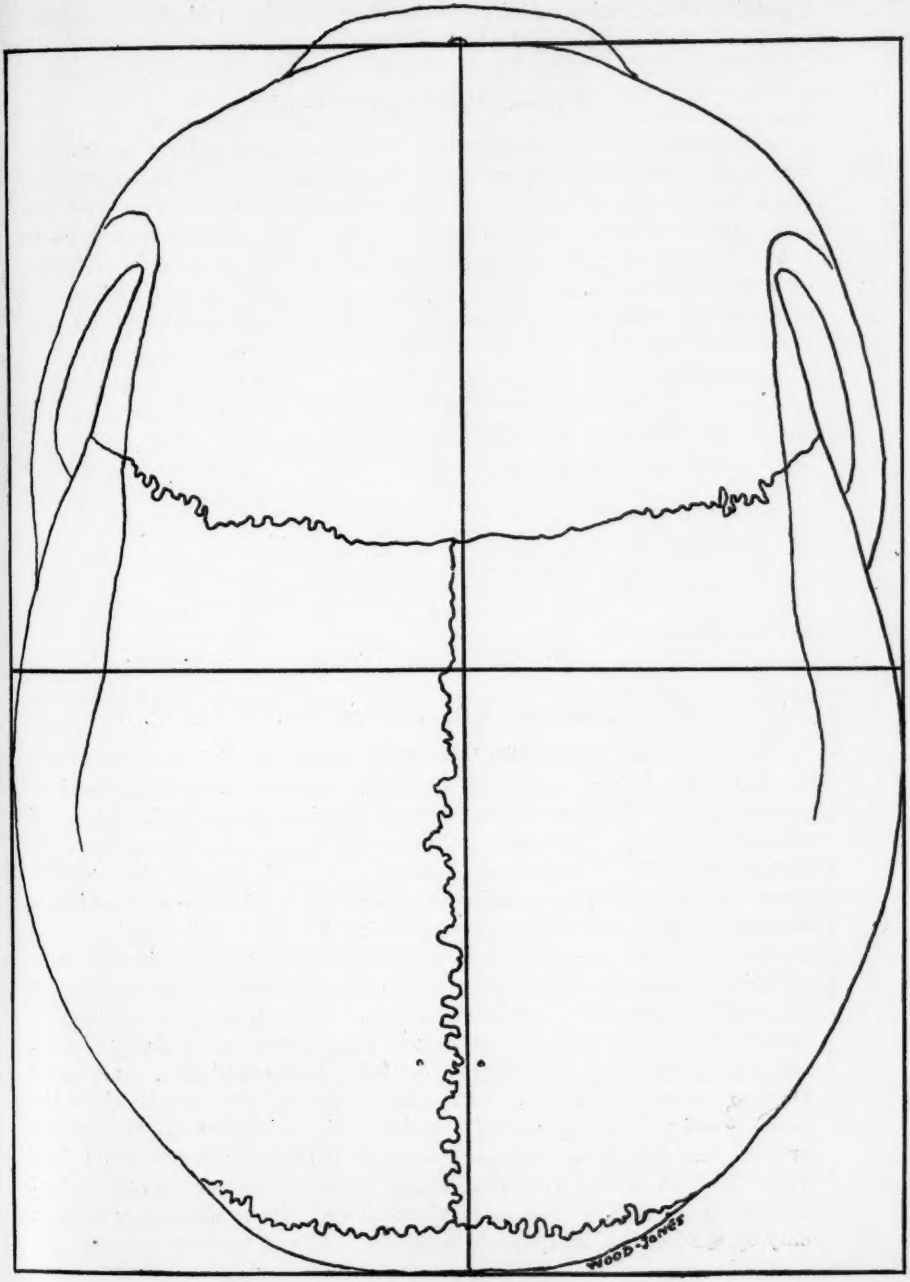

Fig. 4. Norma verticalis.

a position to determine certain criteria of race having a higher taxonomic value than the time-honoured cranial indices.

MATHEMATICAL TREATMENT

The results are of course composed entirely of averages and it is obvious that further mathematical treatment of the large series of figures is necessary. But it has been thought best to defer the computation of standard deviations and correlations until other racial types have been completed and some knowledge has been obtained as to what features hold out promise of being of utility in determining racial criteria. In order to give some idea of the standard deviations prevailing in the present series the following, for the anatomical landmarks on the norma lateralis, are given:

Nasion	Average angle	15·36°	S.D. ±1·707°
	Average distance	89·74 mm.	S.D. ±4·53 mm.
Glabella	Average angle	20·34°	S.D. ±1·909°
	Average distance	98·37 mm.	S.D. ±4·72 mm.
Bregma	Average angle	80·77°	S.D. ±2·296°
	Average distance	111·25 mm.	S.D. ±4·964 mm.
Lambda	Average angle	145·78°	S.D. ±3·495°
	Average distance	100·90 mm.	S.D. ±5·253 mm.
Inion	Average angle	179·44°	S.D. ±4·445°
	Average distance	82·24 mm.	S.D. ±5·252 mm.
Alveolar point	Average angle	338·29°	S.D. ±3·495°
	Average distance	103·05 mm.	S.D. ±5·932 mm.
Spinal point	Average angle	346·48°	S.D. ±1·785°
	Average distance	97·13 mm.	S.D. ±4·894 mm.

CHARACTERISTICS OF THE TASMANIAN SKULL

There is no need to describe the general contours of the skull since these are fully shown in the figures: but it is worthy of note that the whole cranium presents a rounded and well-filled contour which is considerably in advance of that shown in figures usually given in works on physical anthropology. In particular it is important to note in the norma verticalis that the temporal fossae are well filled, a condition extremely different from that which is depicted in Basedow's ideal contour of this norma (4). Again, in the norma facialis the evenly rounded vault of the skull presents a contrast to the reconstruction of a small series given by Parsons (5). Nor is the forehead markedly narrow, the vault of the cranium particularly low or long or remarkably narrow as Barnard Davis has asserted (6). The sutures are typically simple, the greater number of complications occurring in the lambdoid. As Bernard Davis remarked, "in all these Tasmanian skulls the alisphenoid reaches the parietal, but yet only to present a very short articulation with it." The average area of contact in the series reconstructed is 10 mm., but many skulls show an articulation of little more than 3 mm. Apparent temporo-frontal contact appears to be effected, in all cases where suture lines are sufficiently evident, only by the fusion of an epipteric bone.

In the series of nearly 90 skulls of which there are sufficient notes or illustrations the metopic suture occurs three times. The suture between the upper portions of the nasal bones not uncommonly undergoes synostosis in the adult. The nasal bones themselves are small and as Barnard Davis pointed out, they are often "upturned," the free tips pointing rather prominently forward. The narial margins are usually double upon the floor of the narial aperture, the form of which is perhaps best described as being "infantile."

The supra-orbital margin is usually indented by a very shallow notch, a deep notch is the exception, and a foramen is a very unusual occurrence.

The infra-orbital foramen is single in all the skulls I have examined, or of which there are adequate representations. The foramen ovale is typically small, measuring about 5 mm. × 3 mm., and its posterior margin is complete and usually composed of a fairly thick bar of bone. The foramen of Vesalius is of common occurrence. The foramen spinosum commonly falls short of its perfect tubular form by deficiencies of its extra-cranial aspect. The posterior condyloid foramina are typically present; and this is a point of some importance.

The styloid process, as an ossified portion of the skull, is either absent or is reduced to a small nipple of bone that does not project beyond the free margin of the vaginal process of the temporal. The external auditory meatus is, as a rule, narrow from back to front and it is not uncommon for small rounded exostoses to be present on one or more of its walls: the vaginal plate is only moderately thick.

The teeth are large and the palate roomy. The first and second upper premolars are typically double-rooted, and all the upper molars possess three roots and normally show four cusps.

CRANIAL CAPACITY

Having regard to the well proportioned cranium with its rounded contours, one would have been prepared to accept a very fair cranial capacity as being typical of the Tasmanian, but, as a rule, very low figures have been given and there seems to be a general agreement that from 1220–1230 c.c. represents the average. It is rather remarkable that though Hrdlička measured an altogether different series of skulls from that which I have used to construct the present contours, his average measurements of length, breadth, and height very nearly coincide with those that I have obtained. The following table gives Hrdlička's averages and mine. Hrdlička's figures are founded on 37 skulls, none of which is represented in my series of 52.

	Hrdlička	Reconstructed contour
Length	183·7 mm.	182·3 mm.
Breadth	137·1 mm.	136·5 mm.
Basi-bregmatic height	130·75 mm.	130·0 mm.

Using my figures and employing Lee's formula (10) for males, the cubic capacity for the Tasmanian skull equals 1370·79 c.c. By adopting the formula for females it equals 1335·40 c.c. The mean of these is 1353·09 c.c.

High though these figures are in comparison with previous estimates, they are low compared with the result derived by applying the formula of Broca and Manouvrier to the figures obtained by Hrdlička and myself, for using this formula the average cubic capacity equals 1424 c.c. We may either say that these formulae are not adapted to the Tasmanian type of skull, or alternatively that the thickness of the cranial walls is the source of the discrepancy: but it must be remembered that by direct measurement Flower (7) has recorded a skull of 1400 c.c. and Basedow skulls of 1465 c.c., 1450 c.c., 1420 c.c. and 1415 c.c. Sexual differences are not here taken into account; but it is probably correct to say that the commonly accepted low average cranial capacity of the two sexes of this race, like the reputed humanly low-class features of their crania, has been wrongly emphasised, with the result that the Tasmanian has been ascribed a lower place in the human scale than the examination of his cranium warrants.

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VARIATIONS COINCIDENT WITH CONGENITAL ABSENCE OF THE ZYGOMA (ZYGOMATIC PROCESS OF TEMPORAL BONE)

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As far as can be ascertained this specimen is unique.

The skull is practically symmetrical. The zygoma is absent save for a small process on the right side indicating an abortive attempt to form the posterior root. At first glance, the anterior end of the zygoma appears to be represented by a stout process of bone, half an inch long and high, articulating with the malar, but closer scrutiny reveals this little process, itself, as all there is for a malar, the form of which has been efficiently reproduced in turn by the superior maxilla (Plate I).

The normal contour of the skull is interrupted in the temporal fossa by an outward bulging of the squamo-sphenoidal suture. The inferior aspect of the squama is restricted, there is no articular eminence and the glenoid fossa is accordingly shallow. The sphenoid has attempted an anterior boundary to the fossa by two transverse ridges separated by a deep sulcus, which runs backwards and lateral-wards from the foramen ovale. This foramen is situated posterior but barely lateral to the outer pterygoid plate and both these plates are badly developed (Plate II).

The condyle of the mandible is not convex and elongated transversely but small, flat and circular with a well-formed articular disc. The sigmoid notch is very small because it is encroached upon by a very large coronoid process which is markedly everted and deeply grooved medially for the temporalis muscle. The mental tubercles and incisive fossae are very marked, the musculature of the lips is excessively heavy, both jaws are toothless—the upper has a curious gothic arch appearance—and the gums appear flat and densely padded with masticating. The lateral aspect of the angle of the mandible is deeply ribbed and the gonion is well everted. The striking feature is the massive development and fusion of the temporalis and masseter muscles. The absence of the zygoma allows the origin of the temporalis to extend very low upon the squama, and the muscle runs lateral to the condyle, inserts fibres into the articular disc, completely fills the sigmoid notch, has an extensive attachment to the lateral surface of the coronoid process and a stout one into the groove on its medial aspect. The powerful masseter is in the main attached to the stump representing the malar, but a deep posterior portion, rising high upon

the vertical ramus, becomes attached to the articular disc and firmly blended with temporalis, a few horizontal tendinous fibres intervening (figs. 1 and 2).

This fusion may be readily appreciated from the ontogenetic and phylogenetic side (1). The muscles of mastication are developed from a mass which assumes a "Y" shape, the stem becoming the temporalis and the diverging limbs the masseter and pterygoids, the coronoid process intervening. While a few masseteric fibres on the deep aspect of the zygomatic arch frequently fuse with temporalis, these develop to the extent of a definite muscle in some lower animals, according to Toldt.

The absence of the zygoma prompted enquiry as to whether all was well with the ear, and dissection of the petrous bones reveals these interesting variations.

The right external meatus is abnormally narrow. The normal site of the tympanic membrane is occupied by a septum of bone, but a cleft in the superior wall of the meatus is filled with membrane, strands from which bridge across a cavity possessing no ossicles, no attic and no antrum. The Eustachian tube is present and the tensor tympani muscle, very well developed, is inserted into the bony lateral wall of the tympanic cavity. A normal medial wall leads to a vestibule, semicircular canals and cochlea of well-formed, even ample proportions. The left side shows a very narrow external meatus, and a practically normal tympanic membrane, to the medial surface of which and the neighbouring bone is attached a misshapen ossicle, an attempted malleus, like a prehistoric stone axe, the head almost immovably applied to the roof of the cavity. There are no other ossicles, no attic and no antrum. The tensor tympani muscle attached to the deformed malleus is well developed, as also the Eustachian tube. Fibrous strands pass across the middle ear to the medial wall, and, again, the internal ear is normal.

It is rather odd to find the tensor tympani so well formed in apparently functionless circumstances, and the dissecting microscope was used to verify its condition. However, Denker and Kahler's (2) recent handbook alludes to the existence of well-developed tensor tympani muscles in the presence of marked middle ear deformity.

The floor of the orbit is peculiar in sloping sharply downward and forward with no fossa posterior to the infra-orbital margin. The ossification of the lacrimal is deficient, save for the upper portion.

Apart from a chronic inflammatory bone condition in the mid-cranial fossae, the left frontal sinus and the anterior portions of the occipito-atlantal articulations, the subject shows no other exceptional features save good muscular development in a man of seventy-five years.

There is no information as to whether the subject was a deaf mute, and the brain appeared normal to the naked eye.

The literature contains (3) one definite reference, not without practical import and amusement, from Warialda, New South Wales. A gentleman of thirty-eight had been drinking heavily, and one of his friends hit him with a

Fig. 1. Mandible from skull showing absence of zygoma.

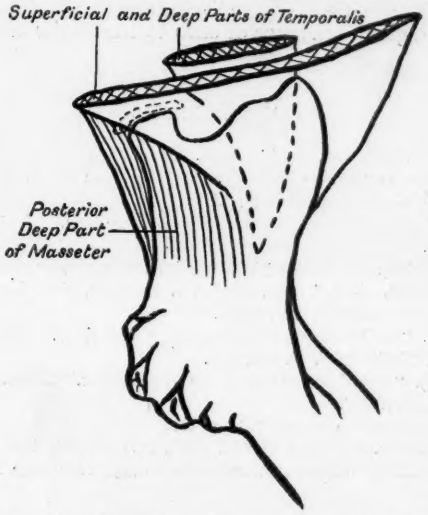

Fig. 2. Disposition of masseter and temporalis muscles on mandible from case showing absence of zygoma.

bottle on the side of the head. The surgeon decided to operate for depressed fracture of the zygomatic arch, but found no arch, the anterior part of the temporalis missing, and a fibrous band replacing the arch from which the masseter arose. He communicated with Prof. Wilson, who had never met a case or a reference.

Regarding the extensive formation of the superior maxilla, Prof. Barclay-Smith (4), in the *Proceedings* of this Society, illustrated a case where the superior maxilla divided the malar to articulate, itself, with the zygoma.

Gruber (5), particularly, and others (6) have written upon anomalies of the malar, and papers (7), to which I have not had access, have appeared upon anomalies of the zygomatic arch. Cases (8) have been recorded where deficiency of the malar has resulted in the arch being incomplete, and the zygoma has been seen separated from the temporal by a suture close to the root, but there is no accurate reference comparable to the present case.

There are numerous points to which no allusion has been made, such as the small plate of the squama, the numerous sutural bones, the formation of the lateral wall of the orbit, and the large size of the frontal process of the superior maxilla. In fact, the more the puzzle of this rather tantalising skull is considered, the more one appreciates the plasticity of Nature's art as a modeller in the medium of bone, not necessarily restrained to the sutural confines of the orthodox text, yet capable of bestowing, as upon the subject in question, a remarkably fine head and face.

The perfection of the internal ear (9), with marked defect of the remainder, is in keeping with the individuality peculiar in the team work of embryological laws, wherein the exquisite, and the defective or monstrous, may be evolved in unison with the tragic indifference of each to the affairs of the other.

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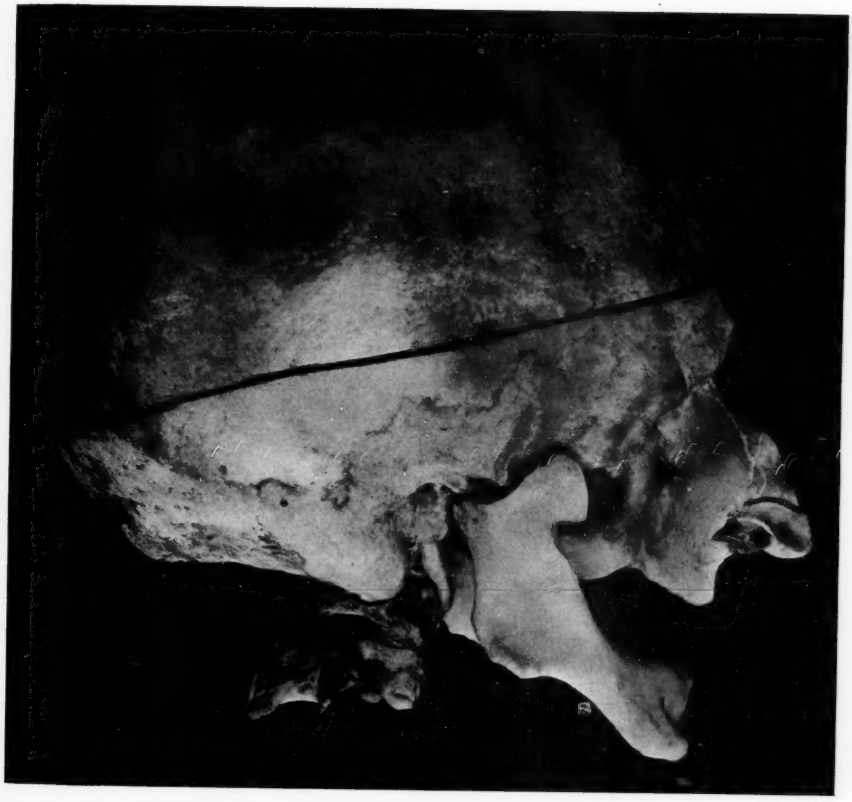
(9) LAIDLAW, P. P. *Journ. Anat. and Physiol.* vol. XXXVII, p. 364, describes absence of internal acoustic meatus and stylomastoid foramen with normal, even large, internal ear.



Lateral view of skull showing absence of zygoma.

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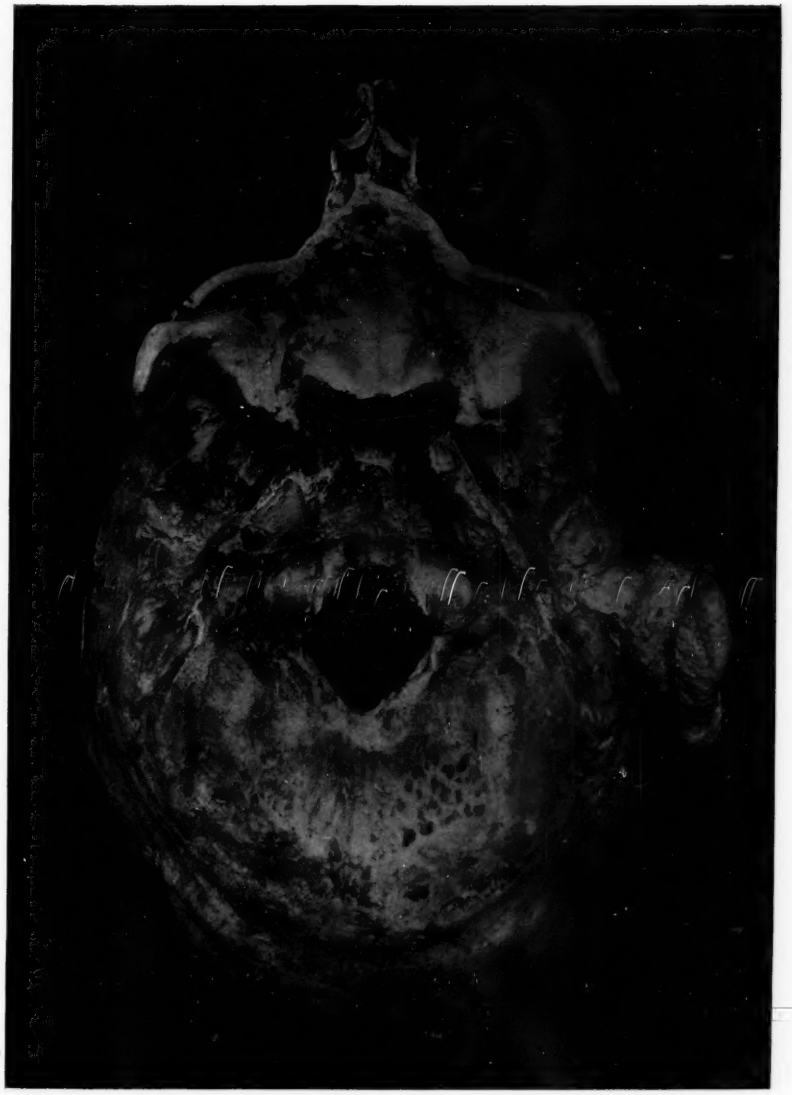

Base of skull showing absence of zygoma.

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THE HINDER END OF THE SKULL IN *MERYCOPOTAMUS* AND IN *HIPPOPOTAMUS MINUTUS*

By HELGA S. PEARSON, D.Sc.
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1. MERYCOPOTAMUS

In 1839 Falconer[1] first described *Merycopotamus* as a *Hippopotamus*. In 1876 Lydekker[2], though placing it among the Anthracotheriidae, still regarded it as a link between that family and the Hippopotamidae; a year later[3] he described its axis and astragalus as almost indistinguishable from those of the anthracothere "*Hyopotamus*" *bovinus* (*Ancodus*) from Bracklesham, but still maintained that the skull and lower jaw revealed affinities with the Hippopotamidae. Recent workers place it without reservation among the Anthracotheriidae; Pilgrim and Forster Cooper have shown that in the Bugti beds of Baluchistan and other deposits of Oligocene or Lower Miocene age in India a rich variety of anthracotheres is to be found, and that while some have the typical five cusps on their molar teeth, and some have only four as in *Merycopotamus*, there are all stages intermediate between these in the degree of reduction of the protoconule.

In figs. 1 and 2 of this paper I have attempted to reconstruct the glenoid, otic and occipital regions of the *Merycopotamus* skull, regions which are not clear in the old lithographs of the *Fauna Antiqua Sivalensis*[4] and not much clearer in the new figure given by Lydekker in 1886[5]. The present reconstructions are based on four skulls in the British Museum (Natural History); three of these, labelled *M. dissimilis* Falconer and Cautley, No. 18441, *M. nanus* Lydekker, Nos. 16551 and 16552, are those figured in the *Fauna Antiqua Sivalensis*, the fourth skull, No. 8583, is that of a young animal from Yenanyoung, Upper Burma.

The structure of these regions of the skull is unquestionably like that of the anthracotheres[6]. The glenoid surface is of the same broad, flat type, smoothly curving upwards postero-laterally at the side of the post-glenoid

[1] *Palaeontological Memoirs*, vol. I, pp. 130–8 *et seq.*

[2] *Rec. Geol. Surv. Ind.* vol. IX, p. 153; see also correction in footnote *Pal. Ind.* ser. X, vol. II, 1883, p. 165 (pt V, p. 24).

[3] *Rec. Geol. Surv. Ind.* vol. X, p. 34.

[4] Plate 67, figs. 1, 3, 5.

[5] *Pal. Ind.* ser. X, vol. IV, pt I, suppl. 1, plate VI, fig. 1.

[6] See descriptions by present writer in *Phil. Trans.* ser. B, vol. CCXV, 1927, pp. 421–7 (*Brachyodus Gorringei*, *B. borbonicus*, *Ancodus velaunus*, etc.); also photograph of *Brachyodus giganteus* Pilgrim, *Pal. Ind.* N.S. vol. IV, no. 2, 1912, plate XV.

process. There is a similar compression of the parts behind the glenoid: the post-glenoid process leans backwards against the wide, plate-like post-tympanic process, the "neck" of the tympanic being squeezed into a flat crest between the two. The exoccipital is splayed out into another flat plate against the back of the post-tympanic process; above this plate, on the posterior surface of the squamosal, is a depressed area which is deeper on some skulls of this genus than on others. The tympanic bulla is similar in shape to that of all those anthracotheres in which I have seen it preserved uncrushed (e.g. *Ancodus velaunus* from Ronzon); its outline may not be quite correct in fig. 1, as it has there been reconstructed from several incomplete specimens, but it must be very nearly correct. The paroccipital process is not preserved intact in any of the skulls: most of it is present in No. 16552, but as it is embedded in the matrix only its postero-lateral border and broken tip can be seen.

The skull differs from that of any anthracothere that I know in the relatively high position of the glenoid surface which is distinctly dorsal to the level of the basis cranii. The glenoid has remained close to the bulla as in *Brachyodus* and not passed out laterally as in *Ancodus velaunus*, nor is the post-glenoid compression so extreme as in the latter form. The post-glenoid process is not so long and pendent as in some anthracotheres; owing to this, and to the higher position of the glenoid, the tympanic "neck" and post-tympanic process project well below the level of the post-glenoid process instead of this process projecting ventrally to them as is usual among anthracotheres.

These characters are probably in part primitive, though the raising of the glenoid surface above the basicranial level may have been a secondary tendency in *Merycopotamus*, as it appears to have been in the ruminants. There is no nearer approach to the construction of these parts in the Hippopotamidae than is found in all anthracotheres.

2. HIPPOPOTAMUS MINUTUS

In 1902 Forsyth Major[1] pointed out the similarity between the pigmy hippopotamus remains collected by Miss D. M. A. Bate in Cyprus, and Cuvier's pigmy hippopotamus[2] (*Hippopotamus minutus* Blainville, *Hyopotamus minutus* Kaup[3]). He maintained that in the shape of the molar teeth this species shows the most generalised condition of all the known hippopotami.

Gervais[4] had pointed out the similarity of Cuvier's pigmy hippopotamus to the West African pigmy hippopotamus *Choeropsis liberiensis* Leidy, and had accordingly named the former *Choeropsis minutus*, but Flower in 1887[5] contested the right of the Liberian form to generic distinction.

[1] *P.Z.S.* 1902, p. 107.
[2] *Ossemens Fossiles*, 1821, 2nd ed. vol. I, p. 322.
[3] *Classification der Säugethiere u. Vögel*, Darmstadt, 1844, p. 78.
[4] *Zool. et Pal. Gén.* 1867–9, prem. sér. p. 250.
[5] *P.Z.S.* 1887, p. 612.

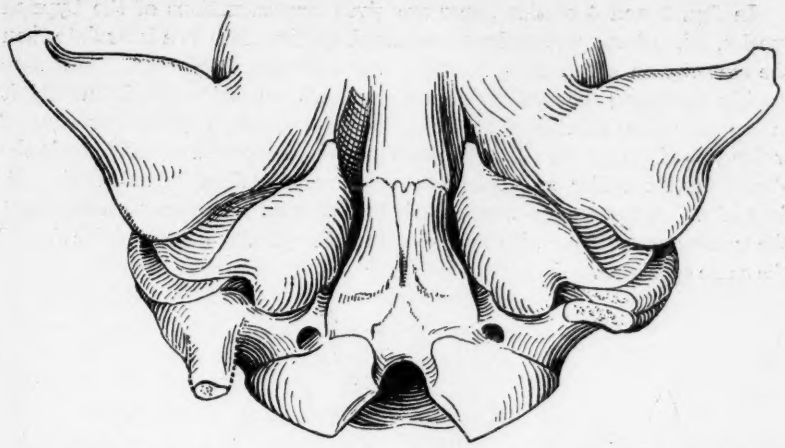

Fig. 1. Reconstruction of the basis cranii of *Merycopotamus*, from three skulls in the British Museum. About three-quarters actual size. Except for section of broken tip, exact shape of paroccipital process (reconstructed with dotted line on right side of skull) is not shown by any of the skulls.

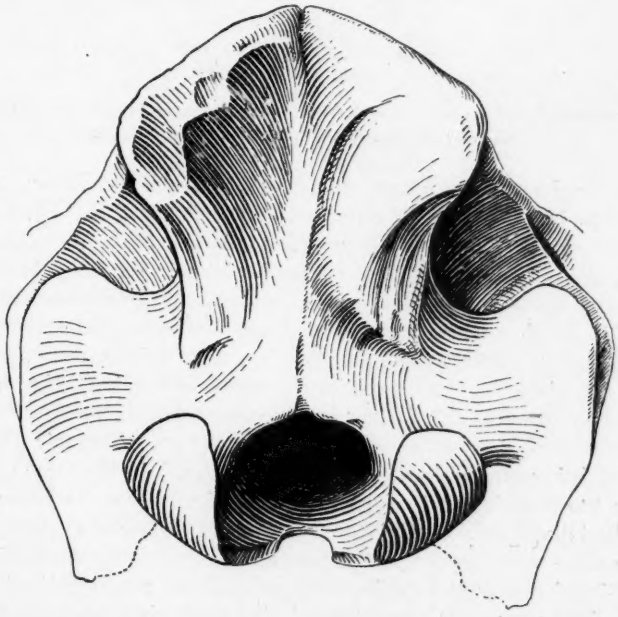

Fig. 2. Reconstruction of the occiput of *Merycopotamus*, from three skulls in the British Museum. About three-quarters actual size.

In figs. 3 and 4 of this paper are given reconstructions of the Cyprian species, taken from two specimens collected by Miss Bate at a later date than the material on which Forsyth Major based his paper of 1902. They were used in modelling the skull of the restored skeleton which stands on exhibit in the fossil mammal gallery of the British Museum, a general account of which was given by Miss Bate in 1906[1]. Each of these two specimens is the almost perfect hinder end of a skull, and except for the tympanic bullae, all four of which are broken ventrally, it has been an easy task to reconstruct the lacking parts of one with the aid of the other, or from the opposite side of the same specimen.

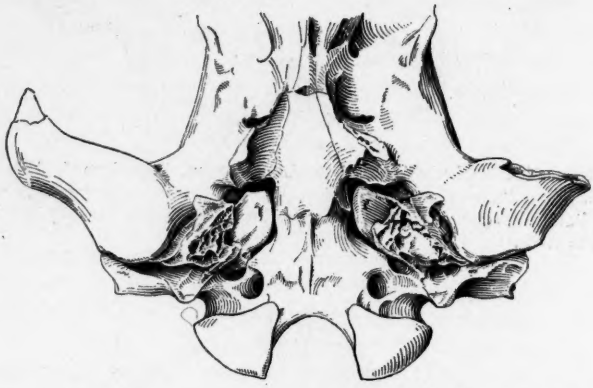

Fig. 3. Reconstruction of the basis cranii of *Hippopotamus minutus*, from two skulls from Cyprus in the British Museum. About one-half natural size.

These specimens show a very close agreement with the hinder end of the skull in the larger species of *Hippopotamus* living and extinct. The post-glenoid compression is extremely similar to that in the anthracotheres (see Pearson, *loc. cit.* pp. 433–5), but the paroccipital process lies in the same transverse plane as the post-tympanic squamosal, the splayed-out part of the exoccipital forming with the latter a single flattened plate which curves backwards at its outer, squamosal border, while its inner, exoccipital part projects down into the small paroccipital process. The occiput is much broader than in the anthracotheres, just as broad compared with the size of the skull as in the larger hippopotami, while owing to the post-tympanic part of the squamosal being pressed back, as described above, into the same transverse plane as the exoccipital, the occipital depression above the latter is very shallow and ill-defined. Furthermore, the glenoid surface of the Cyprian form is of the same laterally elongated type as in the larger hippopotami, narrow from behind forwards and sloping very gradually down on to the face of the post-glenoid process. This type of glenoid is readily distinguishable from that

[1] *Geol. Mag.* N.S. Dec. v, vol. III, 1906, p. 241.

of the anthracotheres, though it might have been derived from one of similar pattern. Between the two fragments from Cyprus, the skull of a West African pigmy hippopotamus, and the semi-fossilised skull of a *Hippopotamus madagascariensis* which I have before me for comparison, there are various slight differences in the shape of the glenoid and the parts behind it. The Cyprian skulls agree, however, at least as well with the Madagascar as with the Liberian skull, and in no way appear to be more primitive or more nearly to approach the anthracotheres or the little Upper Eocene *Cebochoerus* (a possible relative of the hippopotamus stock).

It seems, then, that the claim for the generic distinction of *Hippopotamus minutus* must rest on the characters of the teeth alone.

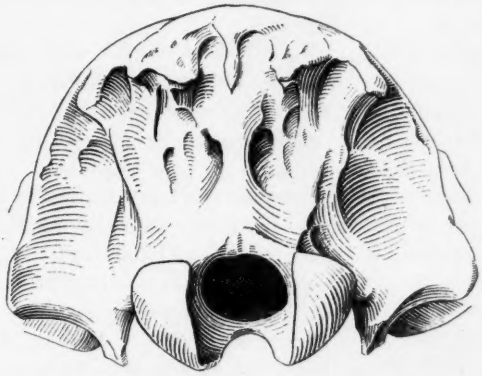

Fig. 4. Reconstruction of the occiput of *Hippopotamus minutus*, from two skulls from Cyprus in the British Museum. About one-half natural size.

SUMMARY

The hinder region of the skull of *Merycopotamus* shows only slight differences from that of all anthracotheres, and these differences are not in the direction of *Hippopotamus*. The hinder region of the skull of the Cyprian *Hippopotamus minutus* is closely similar to that of recent hippopotami and throws no further light on the affinities of the family.

ON THE INNERVATION OF THE PLATYSMA AND THE MANDIBULO-AURICULARIS[1]

By S. B. ADAMS, J. F. G. WHEELER and F. H. EDGEWORTH

In 1918–25 a series of papers on the facial and superficial cervical muscles of the dog and other Mammals was published by Huber. We are not in agreement with some of the conclusions to which he came, and wish to set out the evidence on which we base our views. The dissectional work has been done by the first two investigators, and the embryological by the third, and we are severally responsible for the two parts of this paper.

THE INNERVATION OF THE PLATYSMA IN MARSUPIALS

(In both parts of this paper the term "Subcutaneus colli" is employed to denote the primordium of, or as a collective name for, two or more of the following muscles—Sphincter colli superficialis s. externus, Platysma, and Sphincter colli profundus s. internus.)

The Subcutaneus colli of Marsupials has been described by many investigators. It consists of two strata—the Platysma and Sphincter c. profundus. Admirable figures were published by Boas and Paulli (1908). The Platysma is a continuous sheet of fibres which extends from the neck forwards on the face to the angle of the mouth. The Sphincter c. profundus, of transverse fibres, exists in the head only. Its posterior edge is just behind the jaw.

Kohlbrugge (1898) stated that in *Cuscus orientalis*, *C. maculatus*, *Macropus brunii*, and *Perameles doreyana*[2] the VIIth cranial nerve innervates the deeper layers of the facial musculature and also the deeper and hinder parts of the concha auris (by the R. auricularis posterior). It has no branches posterior to the hyoid bone. Its ventral twigs do not reach the ventral edge of the jaw. The R. laterales of N. cervicales ii–iv anastomose with one another. Those of

[1] The history of this investigation will explain the delay in its publication. In a paper published in 1914 on the development of these and other cranial muscles I gave an account of Kohlbrugge's work and—accepting his statements—offered other explanations of the phenomena he described. I thought it would be well to obtain additional information of the condition in adult Marsupials, but then came the war, and other duties. Five years subsequently Dr Bancroft kindly sent me the heads of several Australian genera, and Mr Wheeler, in 1920–1, investigated *Macropus dorsalis*, *M. ruficollis*, *M. giganteus*, *Petrogale*, *Bettongia* and *Phascolarctos*. But *Dasyurus*, the development of which I had followed, was missing, and publication was postponed. Later on Dr Bancroft was good enough to send this. Then came Huber's paper on *Didelphys* (1924) and it became necessary to get this genus also. I succeeded in obtaining three specimens, two by gift from Profs. Hartman and J. P. Hill, and one by purchase. Mr Adams investigated these two genera in 1925–7. Meanwhile I had investigated *Tatusia novemcincta* and *Manis* (1923). But it appeared advisable to obtain more evidence of the development of the Mandibulo-auricularis, and this became possible by the loan or gift of embryos of the cat, from Prof. J. P. Hill.

F. H. E.

[2] This is the correct name. It had been called *Paradoxurus* in the paper (communication from Prof. Kohlbrugge).

N. cervicales ii and iii pass to the head, of iii and iv to the fore-limb. The branches of N. cervicales ii and iii pass upwards on the face, to the zygomatic arch, crossing the deeper lying branches of the VIIth and innervate the superficial musculature there.

Huber, in association with Hughson (1923–4), found in *Didelphys marsupialis* that unipolar intracranial stimulation of the VIIth nerve caused contraction in the whole territory of the "Gesichtsmuskulatur," whereas stimulation, within the vertebral canal, of N. cervicales i–iv did not cause contraction of the "Facialismuskulatur."

It becomes clear from the text of the paper that this means that stimulation of the VIIth nerve causes contraction of both the facial musculature and of the cervical Platysma, whereas stimulation of cervical nerves does not cause contraction in either.

Huber consequently expressed his disbelief in the statements of Kohlbrugge, stating that if he had "eingehender und sorgfältiger mit der Facialismuskulatur beschäftigt" he would not have come to the conclusions he did.

It is first to be remarked that Huber did not make any anatomical investigations in any Marsupials either of the VIIth (except its R. auricularis posterior) or of cervical nerves. He relied exclusively on the results of experimental stimulation. (In the case of the dog both anatomical and experimental methods were employed.)

Anatomical investigations on a series of Marsupials led to the following results:

In *Didelphys marsupialis* (fig. 1) the VIIth nerve, on issuing from the stylomastoid foramen, gives off the R. auricularis posterior, then a branch to the Interhyoideus s. Digastricus posterior, and then passes forwards on the surface of the Masseter and beneath (i.e. internal to) the Sphincter colli profundus. It breaks up into four main branches which soon subdivide. The R. auricularis posterior vii passes upwards behind the concha auris, and innervates the Platysma behind the concha and the Mandibulo-auricularis. Of the four main branches of the nerve the uppermost passes forwards and upwards, the next two forwards, and the lowest downwards. Finer branches pass from these main ones to the facial muscles and the Sphincter profundus, and very fine ones through the profundus to the Platysma. The most posterior branch innervates the Platysma vertically beneath the anterior border of the concha auris. The Platysma behind that line is, except for the part innervated by the R. auricularis posterior, innervated solely by cervical nerves. There is no R. colli vii. Branches from the first three cervical nerves anastomose and form a plexus, from which a branch passes between the Sphincter profundus and the Platysma, entering the latter vertically beneath the anterior border of the concha auris. An ascending postauricular branch gives off one twig to the concha auris and another to the Platysma just behind and below the concha auris.

A relatively large branch of the IVth cervical nerve innervates the Platysma overlying the Sternomastoid muscle and the parotid gland.

There are numerous anastomoses between the branches of the VIIth and those of the Vth nerve, but there is none between branches of the VIIth nerve and those of the cervical nerves. As stated above, the branches of the VIIth nerve are internal to the Sphincter profundus, those of the cervical plexus external. In one specimen a single small anastomosis was found between a branch of the R. auricularis posterior vii and a branch of the ascending post-auricular branch of the cervical plexus.

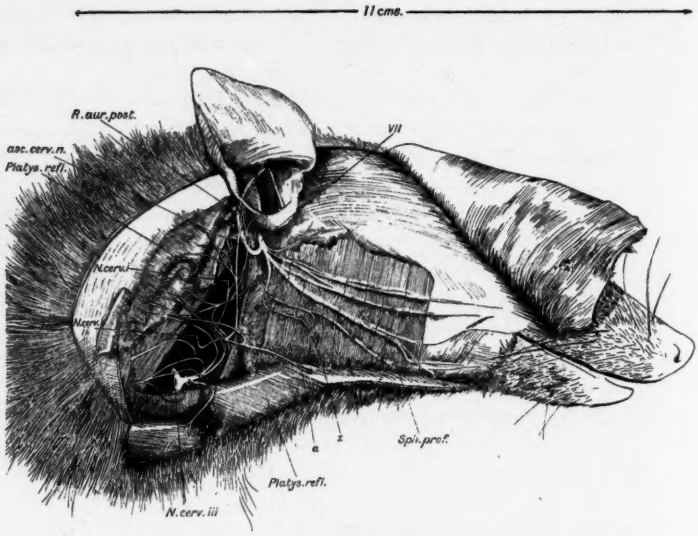

Fig. 1. *Didelphys marsupialis.* A portion of the Platysma has been turned down.

Essentially the same condition exists in *Dasyurus* (figs. 2 and 3), the only difference being that the cervical innervation of the Platysma extends a little further forwards—almost as far forwards as vertically beneath the posterior border of the eye. The lowermost branch of the VIIth descends to the Platysma vertically beneath the external auditory meatus. There is thus some overlapping of the distribution of the VIIth nerve and cervical plexus to the Platysma, but no portion of the muscle was found to receive branches from both sources. There is no R. colli vii.

In *Macropus giganteus*[1], *Petrogale* and *Phascolarctos*, the conditions found were very similar, the only difference being that the cervical nerve branches

[1] In this and the following genera the heads had been cut off rather short, and it could not be determined whether N. cervicalis iii enters the plexus. N. cervicales i and ii, however, were traced in each animal, and as stated above, N. cervicalis iii is present in *Dasyurus*.

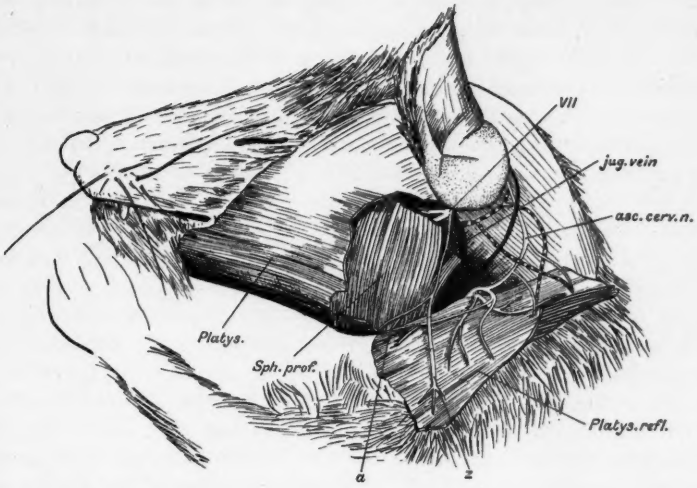

Fig. 2. *Dasyurus maculatus.* A portion of the Platysma has been turned down.

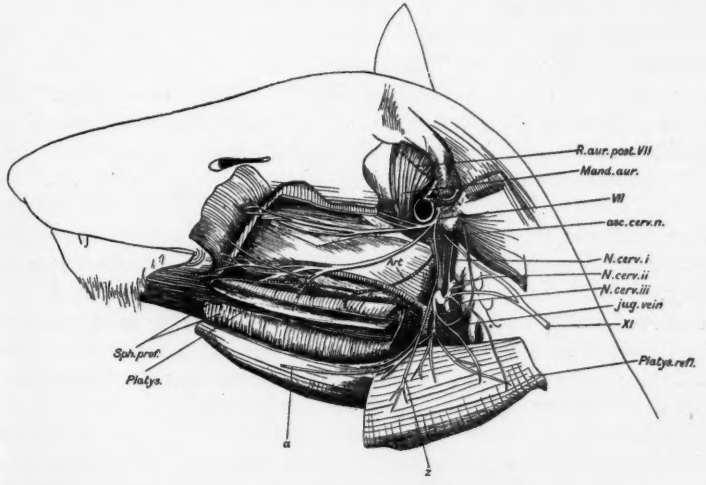

Fig. 3. *Dasyurus maculatus.* Further dissection, a horizontal section has been made through the Sphincter colli profundus and it has been turned down exposing the branches of the VIIth nerve.

passed a little further forwards. In *Macropus dorsalis*, *M. ruficollis*, and *Bettongia* no innervation of the facial portion of the Platysma was found. The entire sheet, facial as well as cervical, was innervated solely by cervical nerves. It is possible, of course, that one or more of these very fine branches perforating the Sphincter profundus were missed, but though carefully looked for they were not found. The conditions are thus similar to those found by Kohlbrugge in *Macropus brunii*, *Cuscus orientalis*, *C. maculatus*, and *Perameles doreyana*. An innervation of the facial portion of the Platysma by the VIIth is replaced by one by cervical nerves. We thus find in eight Marsupial species—*Didelphys marsupialis*[1], *Dasyurus maculatus*, *Macropus giganteus*, *Petrogale*, *Phascolarctos*, *Macropus dorsalis*, *M. ruficollis*, and *Bettongia*—that the VIIth cranial nerve has no R. colli and that, except for the small territory behind the concha auris, its branches do not extend behind the posterior margin of the Masseter. The cervical region of the Platysma is thus innervated solely by cervical nerves. The upper three cervical nerves extend forwards on the face and innervate the Platysma there. Of the genera examined, this forward extension is least marked in *Didelphys*. It is more marked in the others, and in *Macropus dorsalis*, *M. ruficollis* and *Bettongia* no innervation of the facial portion of the Platysma by the VIIth cranial nerve could be found.

We are therefore unable to accept Huber's statement that intracranial stimulation of the VIIth nerve in *Didelphys* caused contractions of the Platysma in the neck, for there is no nerve path by which impulses can reach it, nor his statement that stimulation of cervical roots did not cause any contraction in the Platysma of either neck or face, for branches of these nerves end in the cervical portion of the Platysma and extend forwards in the face and end in the Platysma there.

Our observations are thus in accord with those of Kohlbrugge and at variance with those of Huber, and it must be left to future investigators to ascertain which opinion is correct. Both methods of enquiry—experimental and anatomical—are desirable. S. B. A., J. F. G. W.

The matter might be left here, but some remarks may be added which may afford at any rate a partial explanation of the above described anatomical findings.

I showed (1914) that the Subcutaneus colli is formed as a primordium which develops in the hyoid segment, between the Interhyoideus and the skin. This extends forwards in the face and backwards in the neck, and is the source of the one or more strata of the Subcutaneus colli and of the facial musculature.

No such primordium occurs in lower Vertebrates. It follows that this system of cutaneous muscles has no homologues in non-Mammals. It is, for instance, not homologous with the Constrictor colli of Sauropsida, nor with

[1] Three specimens were examined. They gave concordant results.

the Interhyoideus posterior of Amphibia, which are formed by direct backward extension of the hyoid muscle plate, or of its lower part. Among Mammals backward extension of the Interhyoideus occurs only in *Manis*, where it forms the posterior part of the outer lingual sheath—not the Subcutaneus colli which is formed, as usually, from a primordium between the Interhyoideus and the skin. These statements were altogether misunderstood by Huber, according to whom I had said the "Platysma vom Facialismuskelblastem in der Hyoidregion seine Entstehung nehme." It is then hardly necessary to add that I regard his opinion, for which no embryological evidence was adduced, that the Subcutaneus colli of Mammals is homologous with the above-mentioned posterior extensions of the hyoid muscle-plate in non-Mammals as erroneous.

The Subcutaneus colli spreads backwards into more posterior segments, and the question arises, does it, so to speak, carry its nerve supply with it, i.e. is it wholly innervated by the VIIth nerve, or is this posterior extension innervated partially or wholly by cervical nerves?

In the above-mentioned twelve species (eight genera) of Marsupials, Kohlbrugge and my colleagues find that the latter condition occurs, whereas Huber in *Didelphys* finds the former.

It is obvious that only further investigation can decide the question, but a cervical innervation is by no means *a priori* impossible. Thus the hypoglossal musculature, developed by buds from occipital myotomes, extends backwards in the neck, and is innervated by the hypoglosso-cervical plexus, in which as many as three cervical nerves may take part (*vide* Fieandt).

There are similar instances in the cranial muscles. Thus the Subarcualis rectus iv of Urodela which is developed in the IVth branchial segment (the nerve of which is X_3) and which extends forwards to the Ist branchial bar, may receive branches from X_2 and X_1. The Cucullaris extends backwards into cervical segments and may receive additional branches from cervical nerves. This is a marked feature in Sauropsida.

Recent experimental work by Detwiler (1928) points in the same direction. He showed, in *Amblystoma* embryos, that when a limb was grafted only three or four segments caudally, the normal brachial nerves make a functional connection with it; if at a greater distance spinal nerves which ordinarily supply trunk muscles will build up a brachial plexus in which the intrinsic nerve distribution is essentially the same as under normal conditions.

The innervation of the cervical portion of the Subcutaneus colli described above appears to be an analogous phenomenon.

The forward extension of cervical nerves in the face described both by Kohlbrugge and my colleagues is unique among Mammals. It does not occur in non-Marsupials. It is difficult to account for. Possibly it is of functional advantage.

THE MANDIBULO-AURICULARIS

Schulman (1891) found that the Mandibulo-auricularis of *Myrmecophaga iubata*, *Halmaturus Bennettii*, *Didelphys azarae*, *Sorex araneus*, *Felis lynx* and *Lemur varius*, is innervated by a branch of the R. auricularis posterior vii.

He inferred from this innervation that the muscle "trotz seiner vorgeschoben Lage morphologisch mit den postauricularen Facialisgebiet zusammenhängt."

Huber (1918–25) added to the number of instances in which there is a similar postauricular innervation, and asserted that it is "ein Abkommling der retroauricular Facialismuskulatur," and added that it is developed from the Platysma.

A postauricular innervation, however, is not invariable. The Mandibulo-auricularis has been stated to be innervated by a praeauricular branch of the VIIth in the following genera:

1. *Tatusia* (Bijvoet, E.).
2. *Manis* (E.).
3. *Elephas africanus* (Miss Eales).
4. *Erinaceus* (Michelson[1]).
5. *Hapale jacchus*, *Papio?* spec., *Macacus nemestrinus*, and *Orang-utan* (Paugger).

Huber sought to explain these variations in the path of the nerve by the assertion that in genera where there is a praeauricular innervation the muscle is not a homologous structure and is developed in front of the ear from the Sphincter colli profundus.

Now I had shown (1914) that in *Dasyurus viverrinus* and *Didelphys marsupialis*—where the innervation is postauricular—the Mandibulo-auricularis develops in front of the ear from the Subcutaneus colli[2], i.e. in the position it occupies in the adult, and does not develop behind the ear and then migrate forwards over it to take up a praeauricular position.

In 1923 I showed that in *Tatusia* and *Manis*—where the innervation is praeauricular—there is a similar praeauricular development.

I have subsequently found that the Mandibulo-auricularis of *Felis domesticus*, where the innervation is postauricular. is similarly developed from the praeauricular portion of the Subcutaneus colli. In a 19 mm. embryo (figs. 4 *a–e*) the upper end of the Mandibulo-auricularis is continuous with the praeauricular part of the Subcutaneus colli ·2 mm. below the upper end of the concha auris. The muscle, ·9 mm. long, passes down external to the anterior part of the concha, and then diverges inwards and forwards, towards, though not yet reaching, the primordium of the jaw. The primordium of the Auriculares

[1] This however is denied by Huber.

[2] In my account of *Dasyurus* it was called "Platysma." A better name is Subcutaneus colli, for the sheet at the site of formation of the muscle is a single stratum. Lower down (*vide* the figure I gave) the stratum is separated into Platysma and Sphincter profundus.

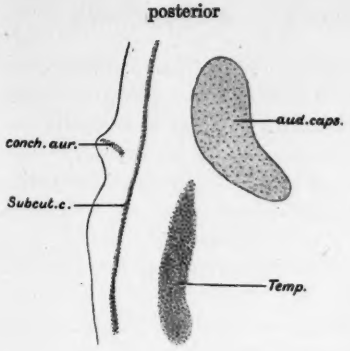

Fig. 4 *a*.

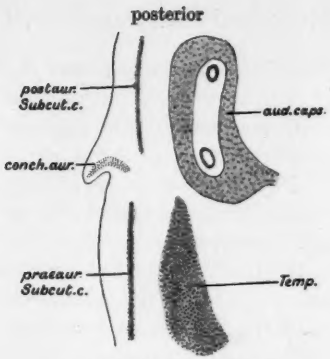

Fig. 4 *b*, ·165 mm. below *a*.

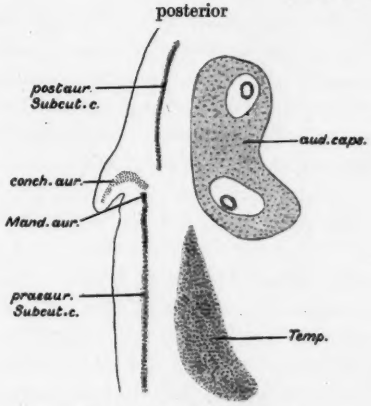

Fig. 4 *c*, ·075 mm. below *b*.

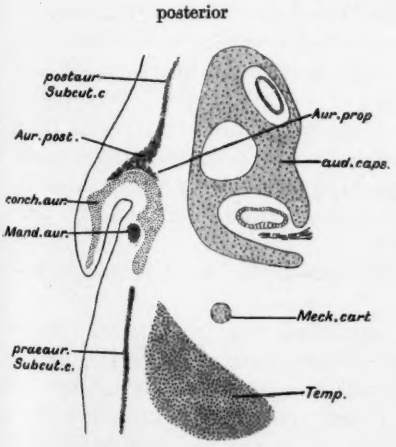

Fig. 4 *d*, ·27 mm. below *c*.

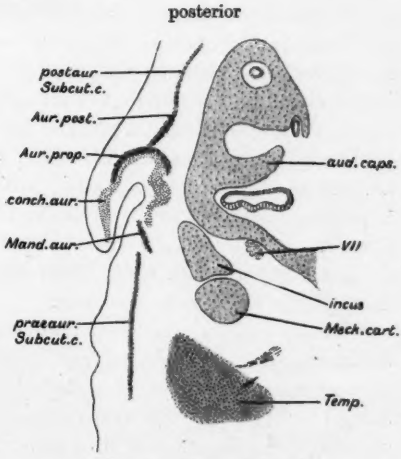

Fig. 4 *e*, ·18 mm. below *d*.

Fig. 4 *a–e*. Five horizontal sections through a 19 mm. embryo of the cat. *a* is the most dorsal.

posteriores, and below that the primordium of the Auriculares proprii, are in process of development from the posterior part of the Subcutaneus colli, posterior to the lower part of the concha auris. The anterior end of the former is attached to the concha auris ·4 mm. below its upper end.

I may add some additional details in regard to the origin and innervation of the Mandibulo-auricularis in the Marsupials dissected by my colleagues. The muscle arises:

1. In *Bettongia, Dasyurus maculatus* and *Didelphys marsupialis*, from the posterior edge of the jaw.

2. In *Macropus dorsalis, M. ruficollis, M. giganteus*, and *Petrogale*, by two heads, one from the posterior edge of the jaw and the other from the hinder part of the zygomatic arch.

3. In *Phascolarctos* from the hinder part of the zygomatic arch.

The Mandibulo-auricularis is innervated by a postauricular branch of the VIIth in all the Marsupials investigated, though not always by the R. auricularis posterior. In *Macropus dorsalis, M. giganteus, Petrogale* and *Bettongia*, the nerve for this muscle leaves the VIIth in the Fallopian canal, emerges at the posterior margin of the tympanic bone, and then passes upwards behind and round the concha auris. The R. auricularis posterior is given off from the VIIth after its emergence from the canal in these as in the other Marsupials dissected.

In *Macropus ruficollis, Phascolarctos, Dasyurus maculatus* and *Didelphys marsupialis*, the Mandibulo-auricularis is innervated from the R. auricularis posterior.

The problem of the innervation of the Mandibulo-auricularis is quite different from that of the Platysma. It is not a question whether a muscle, or part of a muscle, may receive an additional, or supplanting, innervation corresponding to segments into which it has extended. It is simply the question whether—the innervation of a muscle remaining constant, in this case from the VIIth—the path or course of the nerve fibres innervating it is of any importance in determination of its homology.

According to Huber when the Mandibulo-auricularis is innervated by a postauricular branch of the VIIth it is derived from the postauricular Platysma, i.e. has migrated forwards to its adult position, and when it is innervated by a praeauricular branch it is derived from the praeauricular Sphincter profundus.

According to him, then, these muscles are—in the usual terminology—homoplastic and not homologous.

These opinions were not founded on observation. They were, though asserted again and again, merely theories—inferences from the varying course of the nerve, without the slightest embryological verification. And he altogether ignored the observations I had published in 1914 and 1923 showing that the muscle is of constant origin, from the praeauricular part of the Subcutaneus colli. I am of opinion, then, that the Mandibulo-

auricularis is a homologous structure wherever present in Mammalia and that the path of its nerve is variable.

I may mention three similar instances among cranial muscles, and there are others:

In Dipnoi and Urodela the R. mandibularis V. passes outwards behind the ascending process of the palatoquadrate, in Apoda in front of it.

The segmental innervation of the Transversi ventrales or Obliqui ventrales and of the Subarcuales recti of the branchial region is preserved in Teleostomi, whereas in Urodela it has been partially or altogether replaced by one from the R. intestino-recurrens, i.e. though the innervation is still from the Vagus, the nerve fibres take another path.

Meckel (1826) identified one of the masticatory muscles of *Ornithorhynchus* as the Pterygoideus internus. Schulman (1906) found that the muscle is innervated by the R. lateralis of the R. mandibularis V. and not, as usually, by its R. medialis. He came to the conclusion that Meckel's opinion was wrong, and that the muscle is a part of the Temporalis.

This, however, was merely a theory—an inference from the path of the innervating nerve fibres—which he did not put to the test by investigation of the development of the muscle.

I have recently found that the muscle is not split off from the Temporalis and that in early stages it arises from the processus alaris—in both respects agreeing with the Pterygoideus internus of other Mammals. It is only in later stages that its origin extends upwards and the muscle comes into close association with the Temporalis. Schulman's inference was thus erroneous and Meckel's identification correct. Its nerve has a variable path.

We are much indebted to Dr Bancroft for the heads of the Australian marsupials described above, to Prof. Hartman for one of the specimens of *Didelphys marsupialis* and to Prof. J. P. Hill for another, and to Prof. J. P. Hill for the embryos of the cat.

The expenses of this investigation were defrayed by grants from the Colston Research Society.

F. H. E.

UNIVERSITY OF BRISTOL

30 *July* 1928

ABBREVIATIONS IN FIGURES

Figs. 1–3.

VII	Nervus facialis.	*XI*	N. accessorius x.
R. aur. post.	R. auricularis posterior VII.	*Mand. aur.*	Mandibulo-auricularis.
z	most posterior branch of VII.	*Platys.*	Platysma.
N. cerv. i.	Nervus cervicalis i.	*Platys. refl.*	reflected portion of Platysma.
Art.	artery.	*Sph. prof.*	Sphincter colli profundus.
asc. cerv. n.	ascending branch of cervical plexus.	*jug. vein*	jugular vein.
a	most anterior branch of cervical plexus.		

Fig. 4 *a–e*.

aud. caps.	auditory capsule.	*Meck. cart.*	Meckel's cartilage.
Aur. post.	primordium of Auriculares posteriores.	*postaur. Subcut. c.*	postauricular portion of Subcutaneus colli.
Aur. prop.	primordium of Auriculares proprii.	*praeaur. Subcut. c.*	praeauricular portion of Subcutaneus colli.
conch. aur.	concha auris.	*Temp.*	Temporalis.
Mand. aur.	Mandibulo-auricularis.		

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THE EFFECT OF NON-DEVELOPMENT OF THE ALLANTOIS AS ILLUSTRATED BY A CASE OF SYMPODIA

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Cases of Sympodia are related to the group of monstrosities which may be regarded as the result of incomplete development of the hind-gut. There is yet no satisfactory explanation of the teratogenesis of these cases although

Fig. 1. Sympodial foetus.

many theories and suggestions have been enunciated. It appears from a study of the literature concerning these monsters that they repeat the same deviations from the normal in every case, suggesting that they follow some

general law, and the fact which we wish to study in this paper is that in all cases of sympodia the organs, formed from the allantois, fail to develop. The malformation, under discussion, is so named because of limb-fusion.

Before we discuss this irregular development it is well to give a short description of the case which we have studied.

The monster has the appearance of a well nourished foetus of almost full term. The upper part of the foetus is normally developed, but below the

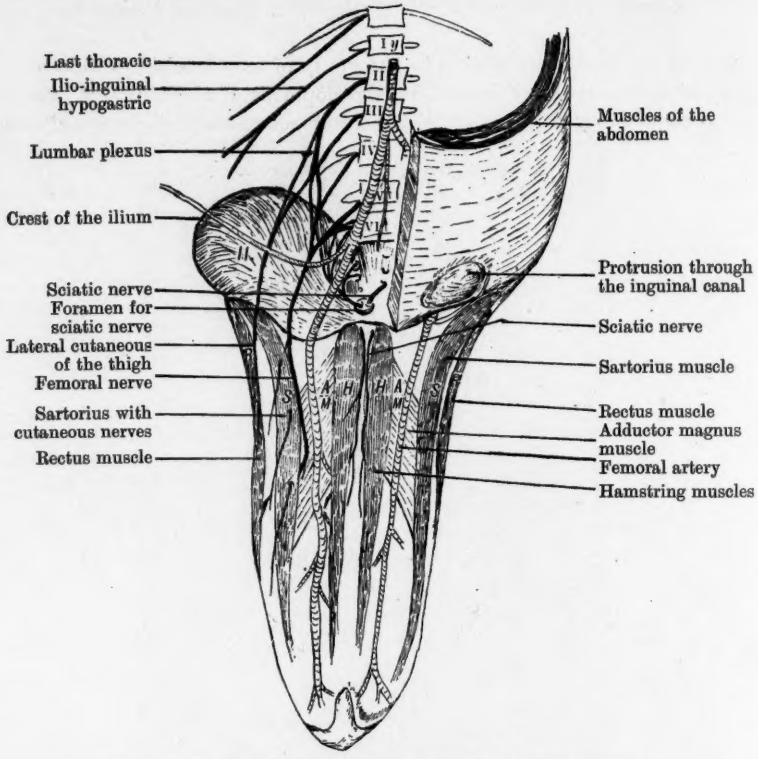

Fig. 2. Dissection of the lower half of the monster seen from the ventral aspect.

umbilicus the trunk gradually diminishes in diameter and becomes continuous with two fused limbs on the end of which there is a single toe with its plantar surface directed ventrally (fig. 1).

The abdominal wall is composed of three muscles with the rectus muscle placed in a normally formed sheath. The abdominal muscles are attached to an aponeurotic arch which, owing to the complete absence of the pubic bones, is stretched between the two iliac spines forming a boundary between the abdomen and the fused lower limbs.

Along this inguinal arch on both sides there are two small projections through the abdominal wall containing on the right side the testicle with its coverings, and on the left the gubernaculum and processus vaginalis, but the left testicle itself is in the abdominal cavity (fig. 2).

Both testicles have a normal blood supply, but the vasa deferentia are joined in the middle of the posterior abdominal wall.

The abdominal cavity is separated from the thorax by means of a normally formed diaphragm, and the contents of the abdomen are as follows: the liver is large, almost filling both hypochondria; the digestive apparatus is composed of stomach, small intestine, caecum with appendix, and large intestine ending in the sigmoid portion. This last part of the large intestine is distended by meconium and is of the size of a large gall bladder.

The pelvis minor is practically non-existent and there is no trace of urinary bladder, ureters, rectum or anus. External urogenital organs are not developed. The site of the kidneys, which are absent, is occupied by large suprarenal glands 3 by 4 cm. in diameter, with big vessels resembling the renal, and the left suprarenal vein crossing the aorta in the manner of a renal vein.

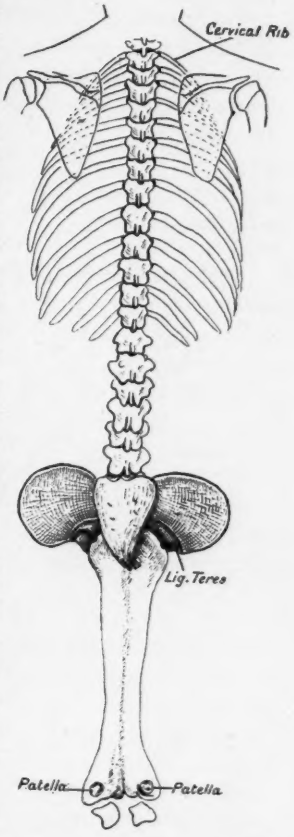

Fig. 3. The skeleton of sympodia, posterior aspect.

The Skeleton. In the upper part of the skeleton a pair of cervical ribs is present and the bones generally are developed and articulated normally. In the lower half the following conditions are found: the ilia and ischia (the pubic bones being absent) are united in front of the sacrum and coccyx which are thrown back as a tail with an external skin appendage. The position of the ilia shows that they never have been rotated forwards and the anterior superior spines are directed laterally and downwards. The internal surface of each iliac bone is slightly convex. Medially the hip bones articulate with the sacrum by their upper portions, but the lower parts are united together, forming one flat bone in front of the sacrum (fig. 3).

Anteriorly the hip bones show a union of the two ischial tuberosities which are turned inwards and situated in the place of the symphysis pubis. The fused hip bones, seen from the back, form a single large acetabulum into which fits the common head of the two fused femora (fig. 3). On this common

head there are two foveae capitulae each with a ligamentum teres, and on the surface of the shaft there is a shallow depression indicating the line of fusion. The distal articular surface of the combined femora is composed of two symmetrical halves articulated with two small bones which can be regarded as the bones of two legs.

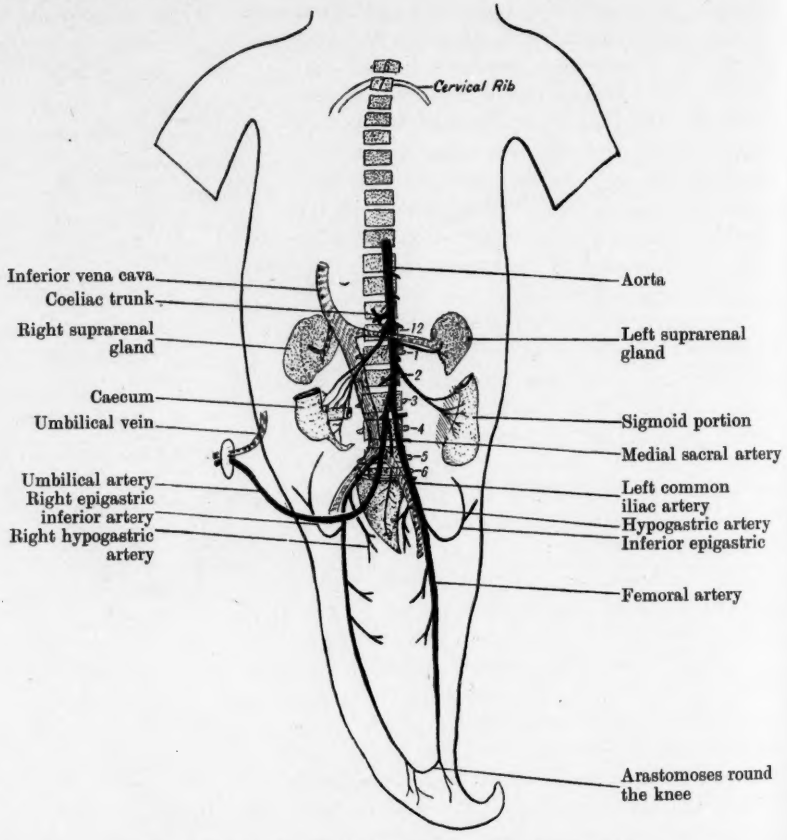

Fig. 4. Blood circulation in the lower half of the sympodia.

The fused femora remain in an unrotated condition, i.e. the anterior surface is placed laterally, the lateral surface looks backwards and the shaft is distorted in such a way that its posterior surface is found in front of the fused limb.

The two patellae are situated on the dorsal aspect of the bone.

Vessels. The state of the circulation in the lower half of the sympodia has been the subject of much discussion on account of the presence of a single

umbilical artery and vein, and also because of the distribution of the vessels in the pelvic cavity. We have found in our case, that the abdominal aorta below the diaphragm gives a coeliac trunk, a superior mesenteric artery to supply small intestines and caecum together with the ascending part of the large intestines, and an inferior mesenteric artery for the rest of the large intestine as far as the sigmoid flexure. There is no connection between these vessels and the umbilical artery. At the level of the third lumbar vertebra the aorta divides into two main branches; the right one, after giving off a medial sacral artery, breaks into a single umbilical artery and a common iliac trunk. The right common iliac gives off a hypogastric and epigastric inferior, and then continues as the femoral artery. The left common iliac after supplying similar branches (except medial sacral) becomes the femoral artery as on the right side. The femoral arteries, owing to the fusion of constituent parts of the thigh, send their branches towards the middle line where they anastomose.

The veins, as shown in fig. 4, are in a state of normal development.

Nerves. In the case of sympodia it is only possible to recognise the constituent structures of the fused limbs by dissection of nerves towards their origin, and after careful dissection it is found that the lumbar plexus is formed by the union of anterior divisions of nerve root from the 1st to the 5th lumbar (fig. 2). The femoral nerve after being formed supplies cutaneous branches for the thigh which are distributed on the lateral and on the antero-lateral surfaces but the main part of the nerve, namely its muscular branches, winds round the femur towards its lateral and extensor surface.

The sciatic nerve after passing through a small foramen in the pelvic floor appears between the hamstring muscles on the ventral anterior surface of the fused limb.

It will be seen from this description that we have found in our case almost the same anatomical structures which have been found in similar monsters, and this similarity of structures allows us to study maldevelopments which are in relation to the hind-gut and, in particular, to the development of the allantois.

Let us suppose that at the end of the third week or at the beginning of the fourth week of development of an embryo the allantois and the cloaca fail to appear from the caudal end of the hind-gut: then we should expect to find an absence of those organs which develop from these parts, i.e. kidneys, ureters, bladder, part of the penile urethra and part of the rectum, and this is precisely the condition which is found in sympodia. Comparative embryology of the allantois and placenta may throw some light on the sympodial monstrosity because the embryonic development of fishes is principally distinguished from that of most higher vertebrates by the fact that neither amnion nor allantois is developed in them.

The fact that non-development of the allantois in fishes is normal, helps us to understand or explain the absence of the urinary organs in sympodia.

It is known that the ureters arise as diverticula from the Wolffian ducts close to the point where the latter join the cloaca with which the allantois is continuous. The urinary bladder develops mainly from the superior part of the anterior subdivision of the cloaca, i.e. from the portion known as allantois, and it is possible to suggest that non-development of the diverticulum which should grow from the entodermal cloaca towards the body stalk may bring about the abnormalities which usually occur in sympodia. It is the rule in sympodia to meet with a single umbilical artery, and it has been suggested that the single artery and vein of the umbilical cord are omphalo-mesenteric vessels, vitelline in origin, and therefore that vascularisation of the placenta in this monster is through the vitelline vessels, but if, as in sympodia, there is *no connection* between umbilical vessels and mesenteric arteries we cannot support that opinion.

We suggest that the existence of a single umbilical artery is the result of the absence of an allantoic diverticulum in the body stalk along which in the normal embryo two arteries grow towards the chorion as allantoic vessels becoming, at a later stage, umbilical arteries; but if the body stalk does not contain the diverticulum there is no necessity for a splitting of the umbilical artery which is to establish the placental circulation.

Non-development of the allantois and cloaca which arise from the hind-gut can be explained by a maldevelopment of the hind-gut which is arrested in its caudal growth at the level of the body stalk, and therefore gives no opportunity for an allantoic diverticulum to enter the body stalk in order to form the allantois, and since the hind-gut fails to reach the tail-end of the embryo no cloaca can be established.

As regards the fusion of the lower extremities it might be suggested that owing to the incomplete descent of the hind-gut, the conditions appear to be favourable to the fusion of the lower limb buds, *because there is now no intervening structure which can keep them apart.* This fusion explains the failure of the limb buds to rotate forwards.

CONCLUSIONS

1. The conditions which characterise sympodia are correlated with an incomplete formation of the hind-gut and in particular with non-development of the allantoic diverticulum and of the cloaca.

2. The hind-gut in sympodia probably never reaches the tail-end of the embryo.

3. The single umbilical artery is explained by non-development of the allantoic diverticulum in the body stalk.

4. Fusion of the lower limbs is probably due to the incomplete development of the hind-gut which has been arrested in its tailward growth.

I have to express my thanks to Prof. D. Derry for his kind help and criticism in the preparation of this paper and to Prof. A. K. Henry for his assistance in correcting it.

A NOTE ON THE KINEMATICS OF THE WRIST-JOINT

By GERHARDT VON BONIN

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An inquiry into the kinematics of the wrist bones has led to results which differ in some respects from the usual descriptions.

The nomenclature of the movements of the hand will be that given by Fick; they will be described as dorsal and volar flexion, and as radial and ulnar abduction. They are thus referred to an axis (or a system of coordinates) situated in the forearm, *not* in the trunk. The position of rest is that in which the longitudinal axes of the forearm and the hand are in one line. (The longitudinal axis of the forearm is a line equidistant from both radius and ulna, the longitudinal axis of the hand is a line passing through the third metacarpal and finger.) The middle position is defined as that position in which the centres of both articular surfaces are in contact.

The range of movement of the wrist-joint in the living is given by Fick as 15° radiad and 40° ulnad, each being reckoned from the position of rest. A few control observations, of a limited number, were made on Chinese students who worked in the dissecting room. The right hand was taken in all instances. With the hand in the position of rest, lines were drawn marking the long axis of the forearm and the hand. The angle these two lines formed in extreme radial and ulnar abduction was measured by means of a protractor. The results are shown in the accompanying table, they confirm what was known before that the range of movability is greater in women than in men.

Range of Movability

	Radiad	Ulnad
♂ (11)	14·5 ± 0·34	29·3 ± 0·26
♀ (6)	21·7 ± 0·25	34·5 ± 0·39

The wrist bones are usually taken to be arranged in two rows, the proximal one consisting of the naviculare, the lunatum, the triquetrum and the pisiform (the latter is of small mechanical significance); the distal row consists of the hamatum, the capitatum and the two multangula. This leads to the conception of a proximal radio-carpal and a distal intercarpal joint. Dorsal and volar flexions are then described as rotations around two radio-ulnar axes which are, so far as is known, parallel and rather close to each other (cf. Fick's *Handbuch*, figs. 162 and 163, vol. III). Radial and ulnar abductions are either given on the basis of Henke's work, using his oblique axes, or (Braus) as involving rotation around a dorso-volar axis in the transverse intercarpal joint

and, concurrently, individual movements of the three bones of the proximal row to which the movements around Henke's axes would only form a rough approximation. This description seems to be the best and shortest for dorsal and volar flexion, but we shall see that for radial and ulnar abduction a different point of view might prove advantageous.

For a detailed study of the movements of the wrist bones stereoscopic X-ray photos were made. I am indebted to Dr Kerr of the X-ray Department for the kindness with which he helped me in this matter. The photos (of the author's right hand) were taken in such a position that the central ray passed as nearly as possible through the head of the capitatum. The distance between the anticathode and the film was 50·4 cm. The results set forth here are based on the study of these X-ray photos, and the sketches accompanying this paper were taken from the films for the right eye.

A kinematic analysis of radial and ulnar abduction will be best understood by starting from the position of rest (fig. 3). It will be seen that in ulnar abduction the carpus moves first (fig. 4) as a whole round a dorso-volar axis near the centre of the head of the capitatum. In extreme ulnar abduction (fig. 5) the rotation round this axis is carried still further. Superimposed on this is a rotation of a few degrees of the triquetrum, hamatum, capitatum, and the two multangula as a whole relative to the lunatum. The capitatum is firmly pressed towards the naviculare which, in its turn, gives room by slightly rotating round an oblique axis, thus getting into an almost straight dorso-volar position. The axes for the other two movements go through the head of the capitatum, so that the shortest description would be to say that the carpus rotates round a dorso-volar axis in the head of the capitatum and that this movement is carried slightly further in the case of the distal than it is in the case of the proximal row.

In radial abduction the first stage (fig. 2) is characterised by a movement of the same series of bones we have just met with, relative to the lunatum and the naviculare. These two bones themselves show only a very small amount of rotation relative to the radius. Going into the extreme position (fig. 1) the lunatum has continued its rotatory movement but only by a few degrees, and the set of five bones has also continued its rotation relative to the lunatum. This, however, has only been made possible by the naviculare turning over round an axis going from radio-dorsal and slightly proximal to ulno-volar and just distal, in order to give room for the two multangula to swing round. At the same time, the triquetrum shows a displacement relative to the hamatum, as has been described already by Virchow.

This analysis does not tally altogether with the usual descriptions. The conception of two clearly defined rows of carpal bones sticking together through thick and thin appears to be misleading, it should rather be realised that the wrist bones can arrange themselves in a variety of combinations when moved in different ways. Thus the old conception of the two rows might remain for dorsal and volar flexion, but for radial and ulnar abduction it seems more

Fig. 1.

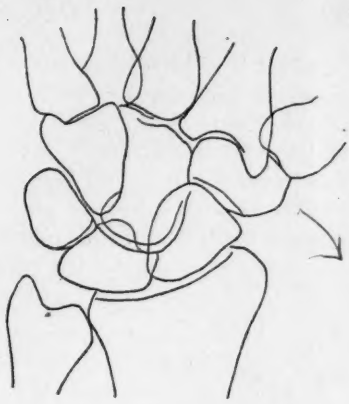

Fig. 2.

Fig. 3.

Fig. 4.

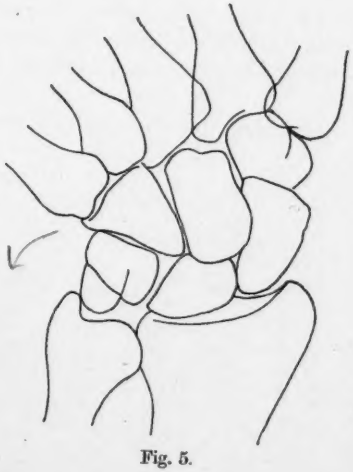

Fig. 5.

expedient to differentiate between the following sets: (1) the five distal bones, namely triquetrum, hamatum, capitatum, multangulum majus and minus; (2) the lunatum which comes nearest to the rôle of an interarticular disc of all the wrist bones; and (3) the naviculare. The joint between the lunatum and its satellite is formed by a ball and socket joint between the naviculare and the lunatum on the one, and the capitatum on the other side, and by two additional joints, radiad and ulnad of it, the one between the naviculare and the two multangula, and the other between the lunatum and the triquetrum. Limited movements round a dorso-volar axis can be executed in this combination of joints.

It will further make for greater lucidity to speak of "main" and "adjustive" movements, the "main" movements being generally those between the distal set of five bones and the radius or the lunatum, respectively, the "adjustive" movements those which are performed by the naviculare and the triquetrum.

Then, counting now from the "middle" position, the shortest description would be to say that from the middle position the carpus moves both ways within certain limits as a whole, but that in extreme abductions adjustive movements come into play, the nature of which have been described above.

MEASUREMENTS OF THE PELVIS IN HINDU FEMALES

By Professor N. PAN

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As there are no records of measurements of the diameters of the female pelvis taken from dead subjects in India, I am publishing the measurements of the pelves of sixty-four Hindu adult female subjects brought to the dissecting hall of the Medical College, Calcutta. With a view to ascertaining the normal average all pelves exhibiting any deformity were excluded from the investigation.

Table A shows the measurements taken in the usual manner at the inlet, cavity and outlet respectively.

The antero-posterior diameter at the brim was taken from the promontory behind to the upper border of the symphysis pubis in front. The oblique diameter from the sacroiliac articulation on one side to the brim at the iliopectineal eminence on the opposite side, the transverse diameter being the widest interval measured from side to side at the brim.

The antero-posterior diameter of the cavity was taken from the middle of the pelvic surface of the third sacral vertebra to the centre of the pelvic surface of the symphysis pubis, and the oblique diameter of the cavity from the upper margin of the greater sciatic notch on one side to the middle of the obturator foramen on the opposite side. The transverse diameter was the widest interval measured from side to side crossing the antero-posterior diameter at right angles.

The antero-posterior diameter at the outlet was measured from the lower border of the symphysis pubis in front to the tip of the coccyx behind, and the oblique diameter from the point of crossing of the sacrotuberous and sacrospinous ligaments on one side to the junction of the rami of ischium and of os pubis on the opposite side. The transverse diameter was the distance measured between the medial borders of the posterior parts of the tuberosities of the two ischia.

The antero-posterior diameter of the outlet was taken without pushing the tip of the coccyx backwards.

Table I. *Measurements of Female Pelvis in Millimetres.*

A. = Antero-posterior diameter. O. = Oblique diameter. T. = Transverse diameter.

Case	Inlet			Cavity			Outlet			Body length	
	A.	O.	T.	A.	O.	T.	A.	O.	T.	ft.	in.
(1)	112	125	112	106	112	100	75	87	75	5	0
(2)	94	119	106	106	112	100	87	62	87	5	6
(3)	106	112	119	106	119	112	75	75	87	4	10
(4)	106	125	125	100	125	119	75	81	87	4	10
(5)	100	125	125	100	112	125	87	94	81	5	5

Table I (*continued*).

Case	Inlet A.	Inlet O.	Inlet T.	Cavity A.	Cavity O.	Cavity T.	Outlet A.	Outlet O.	Outlet T.	Body length ft.	Body length in.
(6)	112	119	125	112	119	112	87	94	100	4	10½
(7)	87	112	112	100	112	100	69	87	75	4	10
(8)	100	112	112	100	100	100	87	94	94	5	0
(9)	100	112	112	87	100	100	75	75	75	4	8½
(10)	100	119	119	100	100	103	87	97	81	5	0
(11)	100	112	119	100	100	100	75	75	75	4	9
(12)	100	112	112	100	106	106	81	87	81	5	3
(13)	119	106	112	100	100	100	81	87	87	5	0
(14)	100	125	125	100	112	112	87	94	100	5	0
(15)	106	112	119	100	100	100	75	81	87	5	0
(16)	103	119	125	100	112	119	87	94	94	5	0
(17)	100	112	125	100	106	112	81	94	100	4	8
(18)	87	100	106	94	100	100	75	87	87	4	10
(19)	100	125	119	100	112	112	87	94	94	5	2
(20)	100	112	125	100	106	112	75	87	87	5	2
(21)	100	112	119	100	100	106	81	87	87	4	9½
(22)	100	119	119	100	100	100	87	94	94	4	9
(23)	106	112	125	106	112	112	87	87	87	5	0
(24)	100	119	125	100	106	112	75	81	87	5	3
(25)	103	119	125	100	106	112	75	87	94	4	7
(26)	100	119	125	100	100	106	75	75	87	4	9
(27)	100	112	131	100	106	112	75	81	87	4	10
(28)	100	119	125	100	106	112	75	81	87	4	11
(29)	100	112	125	100	100	112	75	81	81	4	10
(30)	100	112	125	100	100	106	75	81	81	5	1
(31)	100	112	119	94	100	106	69	75	69	4	9
(32)	87	112	112	87	112	106	75	81	81	4	8
(33)	100	119	125	106	112	106	75	87	87	5	2
(34)	100	125	125	100	100	112	75	87	81	4	9
(35)	100	112	119	87	106	106	62	75	75	4	11
(36)	100	112	112	94	100	100	62	81	75	4	11
(37)	100	106	112	100	100	112	75	75	69		
(38)	112	112	119	106	112	100	75	87	75		
(39)	100	112	119	106	112	112	69	94	87		
(40)	106	106	112	106	100	94	87	75	81		
(41)	112	137	125	119	119	119	100	106	110		
(42)	100	119	125	100	106	112	75	81	75		
(43)	94	119	112	100	100	100	81	75	87		
(44)	94	100	112	100	106	106	87	87	87		
(45)	94	106	119	94	106	106	75	81	75		
(46)	106	125	119	106	112	112	87	87	87		
(47)	95	115	115	96	106	112	84	87	87		
(48)	81	106	100	81	94	100	75	81	75		
(49)	106	119	125	100	112	119	78	87	112		
(50)	100	112	119	108	108	112	81	87	94		
(51)	94	112	119	94	100	106	81	87	100		
(52)	97	119	119	81	100	100	81	87	87		
(53)	100	112	119	100	106	112	81	87	87		
(54)	100	112	119	94	100	106	81	81	87		
(55)	108	125	131	115	115	120	81	87	94		
(56)	106	112	119	94	100	100	87	100	106		
(57)	106	131	137	112	117	125	90	87	90		
(58)	100	112	112	112	119	112	81	81	87		
(59)	100	112	119	100	112	112	75	87	87		
(60)	119	119	112	119	112	119	87	94	94		
(61)	106	112	119	106	112	112	81	87	87		
(62)	112	125	119	112	112	119	81	81	81		
(63)	106	112	125	106	112	112	87	94	94		
(64)	100	125	112	106	119	106	81	94	81		
Average	101	115·5	119	101	107	108·5	79·5	85	86·5		

The following tables show the measurements noted by different authors:

	Antero-posterior	Oblique	Transverse
1. Eden and Holland.			
Brim (plane)	4¼ inch (11 cm.)	4¾ inch (12 cm.)	5¼ inch (13 cm.)
Cavity (midplane)	4¾ inch (12 cm.)	5 inch (12·5 cm.)	4¾ inch (12 cm.)
Outlet (plane)	5¼ inch (13 cm.)	4½ inch (11·5 cm.)	4¼ inch (10·5 cm.)
2. Fairbairn.			
Brim	4½ inch (11 cm.)	4¾ inch (12·5 cm.)	5½ inch (13·5 cm.)
Outlet	About 5 inch (9·5–12·5 cm.)	—	4¼ inch (11 cm.)
3. Williams.			
Superior strait	11 cm.	12·75 cm.	13·5 cm.
Plane of the greatest pelvic dimensions	12·75 cm.	—	12·5 cm.
Inferior strait	11·5 cm.	—	11 cm.
4. Gray.			
Inlet	11 cm.	12·5 cm.	13·5 cm.
Cavity	—	—	—
Outlet	9–11·5 cm.	—	11·5 cm.
5. Cunningham.			
Inlet	4½ inch (11 cm. +)	5 inch (12·5 cm.)	5¼ inch (13 cm. +)
Cavity	5 inch (12·5 cm.)	5¼ inch (13 cm. +)	5 inch (12·5 cm.)
Outlet	4–5 inch (10–12·5 cm.)	4½ inch (11 cm. +)	4¾ inch (12 cm. –)

Figs. 3 represent a mean Hindu female pelvis compared with British and American female pelves represented in figs. 1 and 2 respectively. It will be observed from Table I that the average measurements of the Hindu female pelvis are shorter by about 1 cm. than those of British and American pelves as recorded by different authors. The statistics of 100 full-term Hindu babies show that their weights vary from 3 lb. 2 oz. to 6 lb. 14½ oz., the average weight being 5 lb. 6¼ oz. The average weight of a European full-term baby here is 7 lb. 11¼ oz. and according to American authors that of an American baby is about 7 lb. 4 oz. In the same series of 100 Hindu full-term babies the measurements of the heads are also shorter all round and specially so in the biparietal diameter which is shorter by 1·25 cm. than those of British and American babies.

The body length has been recorded in the first 36 of the cases shown in Table I. It may be noted that the measurements of the pelvis in case No. 2, the tallest subject examined (5 ft. 6 in.), are definitely lower than the average measurements recorded by other observers. On the other hand, in case No. 25, a very short woman (4 ft. 7 in.), the pelvic measurements do not fall far short of the average.

CONCLUSIONS

1. The measurements of a Hindu female pelvis show that all diameters are about 1 cm. shorter than those of a British or of an American female pelvis.

2. As there is a compensatory diminution in the size of the baby's head and in the weight of the baby the average small measurements of the Hindu female pelvis do not necessarily imply difficult labour.

3. The transverse diameter of the space inside the blades of a pair of midwifery forceps when locked should be 1 cm. less for Hindu females than that of forceps intended for British or American females.

4. In statures varying from 4 ft. 7 in. to 5 ft. 6 in. there is apparently no correlation between increase in stature and increase in the measurements of the pelvis.

In conclusion I have to thank Dr Bepin Behari Basak, Demonstrator of Anatomy, for his help in carrying out this investigation.

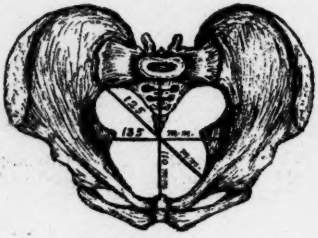

Fig. 1. British female pelvis (sup. aperture).

Fig. 1. British female pelvis (inf. aperture).

Fig. 2. American female pelvis (sup. aperture).

Fig. 2. American female pelvis (inf. aperture).

Fig. 3. Indian female pelvis (sup. aperture).

Measurements of inlet.

Fig. 3. Indian female pelvis (inf. aperture).

Measurements of outlet.

A PRELIMINARY NOTE ON THE RELATION OF SKELETAL OSSIFICATION IN THE HIND-LIMB TO THE INDEX OF CEREBRAL VALUE OF ANTHONY AND COUPIN

By H. A. HARRIS

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Numerous attempts have been made to express in the form of an index the relative proportions of brain and body in various animals. Cuvier (1), more than one hundred years ago, published a comparative table of the ratio of brain weight to body weight. This ratio alone is obviously an altogether inadequate expression of the psychological differences. The fact that the body weight of the mouse is thirty times that of the brain weight, whereas the body weight of Man is forty times that of the brain weight, is enough to indicate this. Brandt (2) stressed the significance of surface area, rather than body weight, in small animals. But even if the brain weight of small mammals be assessed in terms of their relatively larger surface, it still remains relatively great because it is associated with a high metabolic rate and great muscular activity. Manouvrier (3) suggested that brain weight could be analysed into two factors, one of which represented the weight of brain substance (i) devoted to the exercise of intelligence, and the other the weight (m) subserving the functions of the body. Thus the brain weight $(PE) = i + m$. Lapicque (4) indicated that the latter factor (m) is really concerned in particular with the actively innervated part of the body, as distinct from inert deposits of tissues such as fat; and he accordingly modified the formula, so that the brain weight $(PE) = i + km$, where k is a constant for the species.

Keith (5) designated the part of the brain which is present by virtue of the mass of the body as the "corporeal concomitant," and indicated that it decreases with increase in body weight of the animal, so that for the whale or the elephant the "corporeal concomitant" reaches a minimum. Broca (6) had sought a similar expression for Man when he stated that each addition of 10 cm. to the stature yielded a corresponding addition of 5 gm. to the weight of the brain. Marshall (7), basing his results on the data of Boyd, calculated that 10 cm. of stature accounted for an increase in brain weight of 2·4 gm.

Richet (8), in order to avoid errors due to relatively inert portions of the body, compared brain weight with the weight of the liver. This method is open to objection for the relative weight of the liver varies markedly with age and the deposit of fat therein is remarkably inconstant. Manouvrier therefore compared brain weight with the weight of the fresh femur, and found a closer

degree of constancy within any particular species. Dubois (9), working with closely related species, postulated an empirical formula

$$\frac{E}{E'} = \left(\frac{S}{S'}\right)^p,$$

where E and E' are brain weights, S and S' are body weights, and p is an index to be determined.

Dubois found that p ranged from 0·54 to 0·58 with a mean value of 0·56. This led to the formula of Dubois:

$$\text{Brain weight } (E) = K \times S^p,$$

where $p = 0{\cdot}56$ is the "exposant de relation" and K is the "coefficient de céphalisation."

Dunn (10), in a careful statistical survey of the growth of the central nervous system in a series of 156 human foetuses, obtained a formula for the volume of the brain of the general type

$$Y = (aX)^b + c \quad \text{and} \quad Y = (0{\cdot}125X)^{3{\cdot}16} + 1{\cdot}5,$$

where Y = volume of brain, X = crown-heel length of body in cm., and a, b and c are empirical constants.

Scammon and Dunn (11), dealing exclusively with postnatal brain growth in a series of 3000 autopsies, obtained a formula of the general type

$$Y = \frac{x + c}{a + bx} \quad \text{and} \quad Y = \frac{x + 0{\cdot}315}{0{\cdot}09 + 0{\cdot}0692x},$$

where $100Y$ = brain weight in gm., x = age in years, and a, b and c are empirical constants.

Recently Anthony and Coupin (12), instead of regarding brain weight as a function of the approximate square root of the body weight as found by Dubois, or of the approximate cube of a function of the length as found by Dunn, have regarded brain weight as a function of the fourth root of the body weight, and have established a new formula

$$PE' = PS^p \times K,$$

where PE' = calculated brain weight, PS = body weight, $p = 0{\cdot}25$ = coefficient, and K = constant for the species.

This empirical formula yields the calculated brain weight of a reduced image of the adult of the species, i.e. the brain weight of the adult of the species if the said adult were reduced to the size of the young individual considered. Thus, if PE = actual brain weight of the young individual, PE' = calculated brain weight of the reduced image of the adult, i.e. reduced to the same body weight as the young individual, then

$$\frac{PE}{PE'} = \frac{\text{Actual brain weight}}{\text{Calculated brain weight of reduced image}} = \text{Index of Cerebral Value.}$$

For example, if in a given individual the actual brain weight PE = 200 gm. and the calculated brain weight PE' = 150 gm., then

$$\text{the Index of Cerebral Value} = \frac{PE}{PE'} = \frac{200}{150} = 1{\cdot}\dot{3}.$$

Therefore in this individual the brain weight is one-third greater than the brain weight of the reduced image of the adult.

Anthony and Coupin claim that the Index of Cerebral Value gives a definite picture of the urge (*la poussée*) of brain growth. In the human embryo the index increases from 0·13 at the fifth month to 0·60 at term, with a definite rate of increase in the sixth and seventh month. The index reaches 1·0 at about the age of one year and then increases to a maximum of 1·25 at the age of seven. A progressively slower decrease is shown until the index again returns to unity at about 30 years of age. Anthony has also considered the ratio of adult brain weight to the brain weight of the full-term foetus, and has tabulated the length of time necessary for the brain of a particular species to reach its adult size.

The results obtained by this method, based, as the authors admit, on a stratagem, indicated the need for an independent series of observations.

MATERIAL

A group of foetuses, stillborn and young animals, of known body weight and brain weight, were examined radiographically. This material had been used for a series of problems in relation to the question of the growth and development of the skull (13). The ossification centres of the lower limb were carefully recorded, and the Index of Cerebral Value was worked out in accordance with the formula of Anthony and Coupin. The data (Table I) include crown-rump length or age, body weight, brain weight, calculated brain weight and Index of Cerebral Value. The small number in brackets, following the radiographic number, gives the number of foetuses examined. The ossification centres for the lower limb are recorded. In addition, the approximate age of the human foetus or child with the same relative degree of development of ossification in the lower limb is recorded, together with the Index of Cerebral Value for the human foetus or child of that particular age. Thus the standard of comparison is based on similarity of development of the centres of ossification in the hind-limb. For example, the foetal pig (Radio 541) of body weight 400 gm. has an actual brain weight of 14·12 gm. and a calculated brain weight of 22·6 gm. The Index is thus 0·63. The lower end of the femur has just acquired a centre of ossification (Plate I), and corresponds in bony development to a human child at birth. The index for the human child at birth is 0·60. Thus the pig of 19·5 cm. length, about half-way through its ante-natal life of 116 days, has the same ossification in the hind-limb as the human foetus at term. Moreover, the index of cerebral value of this foetal pig (0·63) is approximately the same as that of the human foetus at term (0·60).

Table I. *The Index of Cerebral Value, the ossification of the hind-limb, and the age and index for a human of corresponding ossification.*

Species	Radio No.	Crown-rump length or age	Body weight (grm.)	Brain weight	Calculated brain weight	Index of Cerebral Value	Pubis	Femur distal	Femur prox.	Tibia prox.	Tibia distal	Patella	Os calcis	Astragalus	Cuboid	Cuneiform	Scaphoid	Femur great troch.	Femur less troch.	Tibial tuberosity	Human of equal ossification: Age*	Human of equal ossification: Index
Pig	538 (2)	11·6 cm.	108	3·78	16·28	0·26	0	0	0	0	0	0	+	0	0	0	0	0	0	0	6 mth.	0·24
	539 (2)	11·8 cm.	112	4·21	16·40	0·26	0	0	0	0	0	0	+	0	0	0	0	0	0	0	6 mth.	0·24
	541 (2)	19·5 cm.	400	14·12	22·6	0·63	+	+	0	0	0	0	+	+	0	0	0	0	0	0	Birth	0·60
	542 (2)	20·5 cm.	420	16·38	23·1	0·71	+	+	0	0	0	0	+	+	0	0	0	0	0	0	Birth	0·60
	543 (1)	28·0 cm.	825	33·80	27·12	1·24	+	+	+	+	+	0	+Secy	+	+	1, 2, 3	+	+	0	0	7 yr.	1·21
Cat	965	2 dy.	124	5·0	12·8	0·40	0	0	0	0	0	0	+	0	0	0	0	0	0	0	6 mth.	0·24
	3376	4th wk.	370	16·0	16·6	0·97	+	+	+	+	+	0	+	+	+	1	+	+	0	0	1 yr.	1·00
	3375	4th wk.	380	16·6	16·8	0·99	+	+	+	+	+	0	+	+	+	1, 2, 3	+	+	0	0	1½ yr.	1·09
	3263	5th wk.	425	20·5	17·44	1·18	+	+	+	+	+	0	+Secy	+	+	1, 2, 3	+	+	+	+	7 yr.	1·21
	3261	5th wk.	600	21·5	18·81	1·14	+	+	+	+	+	0	+Secy	+	+	1, 2, 3	+	+	0	0	7 yr.	1·21
	3270	6th wk.	610	24·3	18·88	1·29	+	+	+	+	+	0	+Secy	+	+	1, 2, 3	+	+	+	+	7 yr.	1·21
Lion	3354	Birth	1030	29·2	62·26	0·47	+	0	0	0	0	0	+	0	0	0	0	0	0		7½ mth.	0·46
	1875	2 dy.	1345	44·5	66·62	0·67	+	0	0	0	0	0	+	+	0	0	0	0	0	0	Birth	0·60
Sheep	3240	25 cm.	900	20·5	46·0	0·45	+	0	0	0	0	0	+	+	+	0	0	0	0	0	8th mth.	0·55
	3239	30 cm.	1250	29·0	49·98	0·58	+	+	0	+	0	0	+	+	+	1	0	0	0	0	½ yr.	0·85
Rat		8 dy.	12	0·55	0·88	0·60	+	+	0	0	0	0	+	+	+	0	0	0	0	0	Birth	0·60
		73 dy.	120	1·79	1·56	1·14	+	+	+	+	+	+	+	+	+	1, 2, 3	+	+	+		Puberty	1·13

* Ante-natal age is given in months for Man. Post-natal age is given in years for Man.

Consider the pig at birth (Radio 543). It weighs 825 gm. and has an index of 1·24. The special feature of the ossification in the lower limb (Plate II) is the appearance of the secondary centre for the epiphysis of the os calcis. This epiphysis appears in the human child during the seventh year, at a time when the Index is 1·21. Here again there is a close correspondence between the degree of ossification in the hind-limb and the Index of Cerebral Value for the pig at term and the child in the seventh year.

A similar correspondence is seen for the kittens (Plate III), lions, rats and sheep examined. The rat of 73 days displays commencing union of the three constituent parts of the os innominatum, an event which corresponds closely with the commencement of ovulation and puberty. At this age the Index is 1·14. In the human, union of the three parts of the os innominatum occurs at about 15 years, when the cerebral index is 1·13.

What is the significance of this strange coincidence between the development of the hind-limb and the rate of growth of the brain? The number of animals examined, twenty-one in all, makes it appear improbable that one is misled by that type of random sampling which would correspond to the points of crossing of the curves of brain growth for the different species. It appears that the pig embryo, in the second half of pregnancy, runs through that process of development of the hind-limb which occupies seven years of post-natal life in the human child. The precocity of bone development is accompanied by a similar precocity of brain development. This precocity results in diminished final attainment. The pig embryo has spent the equivalent of the first seven years of human life in a constant environment of amniotic fluid, with but little change of stimulus, and but little variety of response. On the other hand the human child, in the first seven years of post-natal life, is subjected to a change of environment, to a variety of stimuli, to an excessive maternal care; and this results in a corresponding variety of mental responses. The one develops rapidly in a hydro-sphere where new experiences are rare, the other in a world where new experiences are continually happening.

The rat is an interesting example of an animal which is prematurely born. The studies of Strong(14) and Dawson(15) have shown that the extent of ossification in the new-born rat is the same as that of a human foetus of the fourth month. Yet at the eighth day after birth the rat has progressed to a degree of ossification comparable to that of the human at birth. Thus the processes of ossification which are prolonged through the last five months of pre-natal life in the human are telescoped into eight days of post-natal life in the rat. Relative to the human, the rat is born prematurely, the pig and cat post-maturely. Comparative evidence with regard to the Marsupials would be of the greatest value in this respect.

No hasty psychological generalisation can be made from the data already obtained, but it is suggested that this radiographic method of study of the ossification of the hind-limb may throw some light, in association with the

Cerebral Index of Anthony and Coupin, on those problems of behaviour which Coghill (16) has approached from an entirely different point of view. The susceptibility of the animal to formal education may or may not be related to the Cerebral Index and to the rate of ossification of the lower limb.

It may well be asked why the hind-limb has been chosen as a standard of comparison rather than the fore-limb. If the ossifications of the fore-limb be tabulated, no such relationship as that figured in Table I is seen. The hind-limb has retained the distinct mammalian heritage to a marked extent, whilst the fore-limb has been freely modified for specialisation of function. It is interesting that Manouvrier, in his studies on the weight of the brain, should have obtained his most consistent results by a comparison with the weight of the femur, so avoiding many of the difficulties due to differences in the state of bodily nutrition. The results obtained so far from the radiographic method suggest that there are factors of deeper significance than those suggested by Manouvrier. If the hind-limb retains the common mammalian pattern to a greater extent than the fore-limb, why should the ossification of the hind-limb bear a closer parallel to the growth of the brain than that of the fore-limb? Donaldson (17) has stated that the weight of body tissue controlled by one gram of brain substance may have no significance whatsoever. There is no justification for the view that the efficiency of control of the body, or the intelligence of the individual, depends on the mass of body over which a unit of brain substance presides.

The data for body weight and brain weight of the new-born and adult are collected in Table II, together with the Index of Cerebral Value for the new-

Table II. *Body weight: brain weight ratios for adult and new-born.*

Species	Gestation period (days)	Adult body weight (gms.)	New-born body weight	Adult weight / New-born weight	Adult brain weight	New-born brain weight	Brain weight adult / new-born	Adult weight body / brain	New-born weight body / brain	Index of Cerebral Value at birth
Man	280	60,000	3200	19	1360	314	4·33	44	10·2	0·60
Cat	56	3,000	120	25	30	5	6·0	100	24	0·50
Lion	112	135,000	1350	100	250	44·5	5·6	550	30	0·52
Rat	21	330	5	66	2·3	0·2	11·5	143	25	0·28
Rabbit	28	1,463	32	46	10·5	1·2	8·5	139	27	0·34
Pig	114	100,000	826	121	90	34	2·6	1100	24	1·27
Sheep	154	35,000	3400	10	100	52	2·0	350	65	0·82

born of the species. At first it was thought that the data would throw some light on the dramatic events connected with the physiology of the young, such as the opening of the eyes, opening of the external ears, walking and the characteristic reflexes such as scratching. No such relation emerges from the

data, as is shown in the comparison of the pig which walks at birth with the kitten, which lies helpless. It would be interesting to tabulate the ossifications and index of cerebral value in two closely related forms which differ widely in their physiological responses, e.g. the blind, helpless, new-born rabbit and the actively progressing new-born hare. The rat and the guinea-pig afford another pair for comparison, inasmuch as the former with a gestation period of 21 days, and the latter with an extended period of about 68 days, differ considerably in their neo-natal behaviour.

The active growth of the muscular system in the human embryo commences at the 20th week, a time which coincides with the ossification of the bony semicircular canals and with the subjective symptoms of "quickening" in the mother. In the rat the active development of the muscular system commences about the end of the first week, and at this time the ossification of the bony semicircular canals is complete. Moreover, the centre for the os calcis appears soon after ossification of the semicircular canals in the human, pig and rat. The pig of 14 cm. crown-rump length displays the same degree of ossification in the semicircular canals and os calcis as the rat of three days and the human of 24 weeks. Here again there is a close parallel between the development of the lower limb and the development of the periotic bone protecting the vestibular apparatus. It would be of value, in view of the work of Langworthy on the kitten, to ascertain the exact time of myelinisation of the vestibulo-spinal tract in a comparative series of spinal cords. Langworthy (18) has shown that in the kitten the vestibulo-spinal tract is myelinised before birth, whereas the pyramidal and rubro-spinal tracts are myelinised during the third to the fifth weeks of post-natal life, during which time postural tone steadily increases.

Donaldson (19), whose researches into the growth of the Wistar Institute rat afford such a mine of information, has suggested that the rat lives at thirty times the rate of Man. The rat doubles its birth weight in six days; Man in one hundred and eighty days. In relation to the nervous system in particular, Donaldson has considered the increase in the weight of the brain, the decrease in the water content thereof, the accumulation of myelin, the results of Addison (20) on the completion of the Purkinje system of cells and Sugita's (21) determination of the time of attainment of the definitive thickness of the cerebral cortex. To all of these, Donaldson applies the dictum that the rat lives thirty times as fast as Man.

The accompanying data (Table III) show that certain anatomical happenings of the type considered in the earlier part of this paper do not fit into this scheme and it is suggested that there is a marked lack of parallelism in the development of the two forms. Thus so dramatic an event as puberty, which coincides fairly closely with the time of union of the constituent parts of the innominate bone, is seen to be markedly delayed in Man. Man takes seventy-five times as long to reach puberty as does the rat. He takes over one hundred times as long to cut his first permanent molar. On the other

hand, the time of ossification in the periotic bone, the time of ossification of the os calcis, and of the appearance of ossification in the lower end of the femur show a close parallelism.

It is a matter of common knowledge that centres of ossification appear earlier in the female than in the male, and that epiphysial union occurs earlier in the female. Energetic champions of the anatomical virtues of women have repeatedly pointed out that the female brain is remarkably precocious. Boyd (22) states that the brain weight has quadrupled in girls by the age of seven, and that in boys it is not quadrupled until the age of fourteen. On the other hand, growth of the brain persists in man for a longer period of time than in woman. It would appear that the precocity of the female, both as regards brain growth and ossification, is an indication of the earlier acquirement of a common behaviour pattern and of a diminished intellectual impulse. Bischoff's figures illustrating the earlier onset of loss of brain weight in woman, as compared with man, affords another aspect of the same problem.

Table III.

Event	Age from birth in days		Age from conception in days	
	Rat	Man divided by 30	Rat	Man divided by 30
Gestation period	21	9	—	—
Doubling of birth weight	6	6	27	15
Ossification of semicircular canals	7	5*	28	5
Ossification of os calcis	8	6*	29	6
Ossification dist. epiphysis of femur	8	9*	29	9
Cortex mature thickness	20	15–24	41	24–33
Myelinisation near completion ...	30	15–24	51	24–33
Puberty (union of os innominatum)	73	182	94	191
First molar erupts	19	73	40	82

* Ante-natal.

The inherent conditions determining growth, longevity and senescence are still unknown. The problem of development has to be analysed in terms of the antagonistic factors of vegetative reproduction or growth proper, and differentiation for specialised function. The studies of Minot (23) on the ratio of cytoplasmic volume to nuclear volume for a time held some promise. The active study of mitochondria at the present day may throw some light on the growth cycle, and the work of Cowdry (24) and his associates on the mitochondria-cytoplasmic ratio indicates a possible line of approach. It is probable that the radiographic study of the developmental pattern of the ossification in the lower limb on the one hand, together with the pattern of epiphysial union in the long bones and cranial sutures on the other, may lead to generalisations of much value, particularly if the comparative radiographic method be pursued in association with the growth in bulk, and the concomitant processes of differentiation in the brain.

It is many years since Rubner published his *Fundamental Law of Intra-uterine Development*, in which he stated that the energy required to build up one kilogram body weight of a mammalian embryo was constant for all species, except Man. Birth weight is a function of the period of gestation for the mammals as a whole, but Man is a marked exception, in that the rate of growth *in utero* is very small. The growth urge, as regards the brain, has been in part converted into a differentiation urge, and the differentiation urge may be transferred to earlier stages of ontogeny, so that Man, the biological theory of recapitulation notwithstanding, prepares by processes of differentiation *in utero* the nervous mechanism for that life of varied experiences which is denied to the lower forms.

The value of the Cerebral Index of Anthony and Coupin is still to be assessed. The conception of a calculated brain weight proportional to the fourth root of body weight is apparently devoid of any biological basis. Yet the method affords strange results. Similarly the study of parallelism in the development of the ossification pattern of the hind-limb and periotic bone in relation to the development of the brain leads one to believe that the archetype of Owen may yet be resuscitated in modern guise, and that we may still derive some satisfaction from Butler's main thesis: "Living things are active, intelligent agents, personally continuous with all their ancestors, possessing an intense but unconscious memory of all that their ancestors did and suffered, and moving through habit from the spontaneity of striving to the automatism of remembrance."

SUMMARY

1. For thirty-two foetuses and young animals the Index of Cerebral Value has been calculated, and the ossification of the hind-limb tabulated.

2. It is seen that there is a fairly close parallel between the Index of Cerebral Value of any species and the Index of a human of an approximately similar degree of development of the ossification pattern in the hind-limb.

3. No attempt is made at present to reach a generalisation as to the significance of this coincidence.

4. The need for further examination of closely related species with widely different neo-natal activities is indicated; and the time factors in the development of the semicircular canals and in the myelinisation of the vestibulo-spinal tract are suggested as a means of checking the significance, if any, of the results obtained.

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DESCRIPTION OF PLATES I–III

Plate I. Foetal pig. Radiogram No. 541. Crown-rump length 19·5 cm.; weight 400 gm. Index of Cerebral Value 0·63.

The distal epiphysis of the femur presents a centre of ossification. This centre appears in the human at birth when the Index of Cerebral Value is 0·60.

Plate II. Pig at birth. Radiogram No. 543. Crown-rump length 28 cm.; weight 825 gm. Index of Cerebral Value 1·24.

The os calcis presents a secondary ossification centre for the epiphysis. This centre appears in the human at the seventh year when the Index of Cerebral Value is 1·21.

Plate III. Kitten at five weeks. Radiogram 3261; weight 600 gm. Index of Cerebral Value 1·14.

The os calcis presents a secondary ossification centre for the epiphysis. This centre appears in the human at the seventh year when the Index of Cerebral Value is 1·21.

ANATOMICAL NOTES

SKULL SHOWING PERFORATIONS OF PARIETAL BONE, OR ENLARGED PARIETAL FORAMINA

By E. P. STIBBE, F.R.C.S.

This skull is the property of the Horniman Museum; Dr Harrison kindly authorises me to show it for him.

It is a Patagonian skull, though it would be difficult to classify it without the history.

The skull presents several peculiarities, but most notably two large symmetrically placed parietal perforations. The literature of some ten cases of this anomaly was summarised in 1900 by Patterson and Greig, and the possible significance and origin of the condition were discussed. It would appear that the cases recorded may be divided into two groups:

(1) Those where the perforations are in the position of the normal parietal foramina, and appear to be only exaggerations of these.

(2) Those in which the perforations are not in the positions of parietal foramina, and, therefore, more difficult to account for.

The present case would appear to belong to the former category—namely it might well be called a case of enlarged parietal foramina: for the two large perforations are seen to be about three-quarters of the way back along the sagittal suture and close to the mid-line.

In previously reported cases there has been an associated series of anomalies—notably microcephaly, some synostosis of sutures and deformity generally of the nature of plagiocephaly.

This skull, which I am bound to confess did not at first sight appear anomalous, except in the matter of the foramina, does on close inspection fall into line with the others—thus:

Capacity: by direct measurement independently by Dr Young and myself—1200 c.c.; by Stockton and Lee formulae about 1350 c.c.

This great discrepancy would appear to be due to an extreme frontal shallowness: it is in fact an interesting illustration of a case where the three dimensions H.L.B. taken and used for capacity calculation cannot give the capacity because of the extreme disharmony of the frontal region.

The measured length is 182 mm.; height (basi-bregmatic) 131 mm.; breadth 135 mm.

Synostosis:

(*a*) Sagittal suture: synostosed for distance of ½ in. between the foramina. Note in this connection that there is a slight indication of scaphocephaly.

(*b*) Coronal suture: well-marked synostosis of lower part of this suture on both sides.

There is nevertheless no antero-posterior flattening of the skull: the cranial index is 74.

Deformity:

(*a*) Tendency to scaphocephaly as mentioned.

(*b*) A peculiar, though very slight, mid-parietal constriction in front of the foramina—suggesting a minute degree of klinocephaly.

(*c*) Slight flattening of parietal bones near mid-line.

(*d*) Slight plagiocephaly; convexity to right side.

Note also the straight horizontal parieto-temporal suture—a character of simian and primitive skulls—and a character which I am disposed to associate with limitations of growth.

Of possible explanations of these openings, trephining and pathological causes may probably be ruled out at once. It is specified in certain of the reported cases that large meningeal vascular grooves may be traced on the inner surface of the skull to the perforations; and writers, therefore, surmise that large emissary vessels have interfered with the growth of the parietal bone. It is interesting that this skull exhibits such decided anomalies of growth all in the direction of hindrance.

SKULL SHOWING EXAGGERATED GROOVING OF TEMPORAL REGION

By E. P. STIBBE, F.R.C.S.

For this exhibit, as for the last, I am indebted to Dr Harrison of the Horniman Museum.

The skull is an exceedingly well-marked Eskimo type—showing the characteristic high scaphocephaly, large face, broad palate, powerful muscular markings, large pyriform aperture and other Eskimo characters.

The special feature to which I desire to draw attention is a deep and wide groove commencing on the outer surface of the great wing of the sphenoid, running upwards and backwards across this and the anterior angle of the parietal bone and dying away gradually on the latter bone.

Examination of a large number of skulls shows the presence of this groove—though in a less marked form—in rather over 50 per cent. of skulls; it seems to attach itself to no race, and to no particular shape of skull, being impartial in its

appearance in dolichocephalic and brachycephalic types. It is, in fact, the sphenotemporal sulcus of Gustav Schwalbe. This author described in the temporal fossae of men and other mammals certain markings corresponding to the inferior frontal, and first, second and third temporal gyri, and to the sylvian and first and second temporal sulci. In the exhibit the inferior frontal and first temporal gyri are readily seen, and the sylvian and first temporal sulci. (The deep groove corresponds to the elevation of the posterior border of the lesser wing of the sphenoid on the interior of the skull; but of course the latter fits into the stem of the sylvian fissure.)

Still more can be discovered by the sense of touch: by running the finger lightly over the temporal bone behind the main sulcus, the three temporal elevations and two corresponding depressions can be most definitely felt.

By examination of this and other skulls—two of which were exhibited for comparison—I have no doubt that in a large percentage of cases one can read the surface of the brain on this part of the skull.

Schwalbe enunciated a law that where the vault is uncovered by muscle, or only covered by such light "flächte" as the frontalis and occipitalis, there the bone is thick and the outer surface smooth: while in the region of pressure of the powerful temporalis the thin skull shows external markings of the brain-pattern.

Here we have a skull showing extreme ruggedness and power of the temporalis muscles, and associated with this a remarkable distinctness of the impressions of the brain; leaving one with little doubt as to the correctness of Schwalbe's conclusions, though at a loss to give any clear reasons for the association.

A CONTRIBUTION TO THE MUSCULAR ANATOMY AND CERTAIN RACIAL DISTINCTIONS OF BUSH NATIVES

By FRAU Dr HELLA PÖCH

[*The communication is an abstract of the account given by Dr Pöch to the members of the Anthropological Society of Vienna, at the Congress held in Salzburg in September*, 1926. *The original paper was published* in extenso *in the Proceedings of the Congress. It should be remarked that the authoress is the widow of the late Dr Rudolf Pöch, whose contributions to physical anthropology and to ethnology, more particularly in relation to Africa, are of the highest value.*]

A DEMONSTRATION was given in September, 1926, at Salzburg on the bodies of two South African Bush natives, a male and a female respectively. They died as long ago as 1909, when Dr R. Pöch was in the Kuruman District of Cape Colony. Both died within the space of a few days, but their exhumation was not carried out until a month later.

The male cadaver measured 4 ft. 8 in. in the supine position. Marked lumbar convexity (forwards) of the vertebral column is recorded, and in general, the external features tally with those known to characterise such natives. The head is long and narrow.

The female subject was smaller and slighter than the male. Gluteal steatopygia was still evident at the time of dissection. The proportions of the head resemble those of the male.

The paper proceeds to deal with a number of muscles, and from these a selection has here been made.

1. The M. pectoralis major is characterised by the distinction of the clavicular portion from the remainder of the muscle. The two parts are clearly separated.

2. The M. flexor brevis digitorum (pedis) consists of two layers, superficial and deep respectively. From the more superficial layer, spindle-shaped muscular slips pass forward to become tendinous and as tendons they proceed to the extensor aponeurosis of certain of the toes. They are of the nature of lumbricals, but the four normal lumbricals are also present. Of these additional lumbricals, the right foot has two (for digits II and III), while the left foot has three (for digits II, III and IV).

The deeper stratum of the M. flexor brevis digitorum sends perforated tendons to precisely the same digits as those to which the additional lumbrical slips pass.

It appears that the muscle supplies no tendon at all to the hallux nor to

the Vth toe in either foot. And in the right foot it sends no contribution to the IVth toe.

In the remaining paragraphs there will be found certain notes on the anatomy of the external genitalia in the male and on the steatopygia of the female. In the former instance, the authoress describes a fibrous band so disposed about the penis as to form an annular ligament supplementary to the suspensory ligament.

In the gluteal region of the female subject the fat was distributed in a definite manner differing from its arrangement in Europeans. The essentials of a racially distinctive steatopygia thereby come to light and they are enumerated as follows:

(1) A distinct adipose mass over the iliac crest.

(2) A principal mass in the central part of the buttock on the M. gluteus maximus. The sacral and coccygeal regions are distinctly less well covered.

(3) At the hips properly so-called, no accumulation of fat, although a deposit is situated just dorsal to the trochanter.

(4) No intermuscular deposits of fat.

The authoress notes that the male subject presents traces of a corresponding disposition of gluteal fat, though the "iliac" mass is said to be absent from the male.

[The authoress certainly seems to have discovered an anomaly of extreme rarity in the form of the supplementary lumbricals. The literature on the M. flexor brevis digitorum is voluminous, and if, as is to be hoped, it is scrutinised in a later publication, there should be taken into account certain memoirs not given in the bibliography, namely, the extensive and comparative works of Sawalischin and of Loth. W. L. H. D.]

CONCERNING THE COURSE OF THE EFFERENT MANDIBULAR ARTERY IN *CERATODUS*

A CORRECTION

By EDWARD PHELPS ALLIS, Junr.
Menton, France

In an article published in the October number of this *Journal* (vol. LXIII, part 1), entitled "Concerning the Pituitary Fossa, the Myodome and the Trigemino-Facialis Chamber in Recent Gnathostome Fishes," the efferent mandibular artery of *Ceratodus* is said to be shown, in Greil's figures of this fish, lying antero-lateral to the otic and ascending processes of the quadrate. This is wrong, for it is actually shown running upward and forward posterior and then mesial to the entire quadrate. This relation of the artery to the otic process would seem to definitely establish that the otic process of the Notidanidae is the homologue of the otic process of *Ceratodus*, as de Beer (1926) concludes, and that both of these processes are the homologues of the metapterygoid process of the Holostei and Teleostei. The lateral wall of the trigemino-facialis chamber of the latter fishes cannot therefore be the homologue of the otic process of *Ceratodus*, as I have heretofore considered it to be. This does not, however, seem to affect my conclusion that the lateral wall of the trigemino-facialis chamber is developed from the post-trigeminus branchial rays of the mandibular arch, for these rays are not otherwise accounted for, the otic and ascending processes both being developed either from the pre-trigeminus branchial rays of the arch, or from the antero-lateral bounding edge of the groove on its external surface, which lodges the artery and nerve of the arch. The antrum petrosum laterale of *Ceratodus* and the Urodela would, however, include a lateral space not contained in the trigemino-facialis chamber and latero-pituitary space of the Holostei and Teleostei.

REVIEWS

Monographs of the American Society of Mammalogists. No. 1. *Anatomy of the Wood Rat.* By A. B. HOWELL. (London; Bailliere, Tindall & Cox: Baltimore; The Williams & Wilkins Company.) 1926. 6″ × 9″. Pp. x + 225. 3 Plates. 87 Figs. Price 22*s.* 6*d.* net.

The American Society of Mammalogists has outlined a series of monographs on the mammals of North America, of which *The Anatomy of the Wood Rat* by A. Brazier Howell is the first. The systematic position of the wood rat (*Neotoma*) and its subgenera are considered in detail, with reference to their habits and external features.

The anatomy of the muscular, alimentary and urogenital system is followed by a detailed description of the skeleton. Muscle action and limb motion are discussed at length and an attempt is made to homologise the muscles of the fore and hind limbs. Subgeneric variation is illustrated by three tables relating to the skeletal, muscular and non-muscular differences.

Jayne's *Osteology of the Cat* set a high standard for American Comparative Anatomy, and should serve as a model for these monographs. It is suggested that a few selected radiograms be included in the subsequent editions, both as a means of displaying the relation of the skeletal to the soft parts, as a means of displaying generic differences, and still more, of illustrating the distribution, size and degree of fusion of the epiphyses during the various stages of growth. Structures which are of peculiar interest to the physiologist, apart from the vagaries of fashion, such as the thyroid and suprarenal glands, should have a brief mention as to shape, size, site and vascular supply.

The Matrix of the Mind. By F. WOOD-JONES and S. D. PORTEOUS. University Press Association, Honolulu.

Those who have already taken the opportunity of probing into the mind of Prof. Wood-Jones through the medium of his published papers and essays will have learnt that it contains a large element of originality. For this reason alone, prospective readers may with certainty anticipate an unusually pleasant study when they take up a new book by this author. *The Matrix of the Mind* was written, as the preface tells us, with the aim of blending "the subject-matter and view-points of two sciences which have the same physical structures as a basis," i.e. neurology and psychology. Further, the publication of this book is regarded by the authors as a necessary preliminary to the correlated study of the problem of racial differences which is to be carried out at the University of Hawaii.

The book is in no way intended to be a systematic treatise. It is written in essay style. This has enabled the authors to escape many of the difficulties which otherwise would be encountered in writing a book of this kind, for the reader is credited with a certain elementary knowledge of anatomy without which he would find it impossible fully to appreciate some of the discussions. A survey of the chapter headings at first suggests that the essay style has been overdone, for they give an impression of a hotch-potch of subjects which bear no definite consecutive relation to one another. However, this is not the case, at least for the first forty-three chapters, which are contributed by Prof. Wood-Jones. But there seems to be just cause for criticism on these grounds as regards the last twelve chapters, the contribution of Stanley D. Porteous, Professor of Clinical Psychology at the University of Hawaii. We find it difficult to understand what was the aim which the latter author had in mind when he wrote Part 2 of the book. It is a rather disconnected series of chapters which seem to bear no clear relation to the first part. It would have been better, we think, if the end of Part 1 had also been the end of the book.

As regards Part 1, we feel that this is essentially a book to be read and enjoyed. It is a book in which the subject of neurology is dealt with in a remarkably stimulating and even intriguing manner and from which may be derived a fund of suggestive hints and novel points of view. There are no doubt many conclusions and suggestions which will at once arouse dissentient criticism, such as the theory of the accidental inversion of the vertebrate retina (a paper which appeared recently in the *Journal of Experimental Physiology* indicates that the inverted type of retina may be an essential preliminary to the development of colour vision), the implication that the crocodile has a pallial representation of vision, the impatience with geneticists for refusing to accept the inheritance of acquired characters as an established fact, the suggestion that the functional rôle of the organ of Jacobson in Mammals is related to food-getting in the dark, and so on. But, indeed, Prof. Wood-Jones' attractive style largely disarms criticism of details such as these, and after reading his book we feel a sense of gratitude to him for his charming essays. They will be found welcome by neurologists and psychologists in general, and especially by medical students who are looking out for an unusually lucid and stimulating introduction to the study of neurology.

One more point—the consistent use of the word "nucleii" throughout the book is rather troubling to a mind with a sensitive matrix.

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THE PROTECTIVE AND DISCRIMINATIVE DIVISIONS OF SENSATION

By JOHN S. B. STOPFORD, M.D., F.R.S.
Professor of Anatomy, University of Manchester

Our conception of sensation has been completely revolutionised by the researches of Head, and the principal observations upon which he based his conclusions have been corroborated by many workers. It was Head who initialled the division of the sensibility of the skin into two systems, terming them epicritic and protopathic. He found that protopathic sensation consists of the cruder elements of sensation, which appear more primitive and necessary for protection and awareness than epicritic forms, the latter embracing the higher elements concerned with discrimination and the testing of objects by feeling and handling them. It has been suggested in consequence that epicritic and protopathic sensibility manifest two stages in the phylogenetic history of man, and the observed facts with reference to cutaneous sensation lend considerable support to such a contention. When we turn to the third system described by Head, that of deep sensibility, we are confronted with obvious difficulties of harmonising it with the attractive scheme proposed for cutaneous sensation. A closer study of deep sensibility and the application of Head's methods in investigating it, has shed light upon the difficulties and brought forward much evidence in support of his hypothesis with reference to the dual nature of cutaneous sensibility.

My own researches (2, 3) have indicated the existence in deep sensibility of two systems, which are exactly comparable to those shown to be present by Head in the skin—the one composed of the elements of sensation concerned with protection, and the other with discrimination. Since, for anatomical reasons, it is rarely practicable (4) to isolate the sensation of the skin from that of the subcutaneous tissues, it has appeared justifiable to combine these two comparable systems and so procure a simple subdivision of sensation into two parts:

System I A system composed of the protective elements of sensation in which recovery occurs early and is more perfect, after suture of a peripheral nerve	Recognition of (*a*) Pain, whether induced by prick or excessive pressure (*b*) Extremes of temperature (*c*) Tactile pressure
System II A system composed of the discriminative elements of sensation, in which recovery occurs at a later time and is less complete and perfect	Power of (*a*) Localisation (*b*) Discrimination (*c*) Recognising position and passive movement Recognition of fine differences of temperature Appreciation of the lightest forms of touch

Such a subdivision of the elements of sensation, in the light of our knowledge of the sensory centres, inevitably invites us to think of the thalamus and the sensory cortex. The latter is concerned with the higher discriminative functions which are essential for the examination of objects by touch. It is necessary for the appreciation of all spacial relations, for the power to recognise similarity and difference, and for the recognition of stimuli of graduated intensity whereby we are able to distinguish differences in intermediate temperatures. After destruction of a large part of the sensory cortex, stimulation with the finer tactile hairs is not recognised, as this requires considerable discrimination. Consequently it is manifest that System II demands the normal functioning of the sensory cortex. The older sensory centre, the thalamus, is a centre for awareness and concerned with the protective, affective and non-discriminative aspects of sensation. Painful stimuli and the extremes of temperature mainly appeal to the thalamus, but although recognised (in a typical "all-or-nothing" manner) in the absence of the sensory cortex, there is no ability to compare sensations, to estimate their intensity or to localise accurately the point stimulated. Furthermore, such accompaniments of the first stage of recovery after suture of a peripheral nerve as overaction are manifested when the thalamus is released from the sensory cortex by widespread destruction of the latter. Thus it appears that the elements of sensation composing System I make their appeal to the thalamus.

There are therefore reasons for terming System I the protective or thalamic division, and System II the discriminative or cortical division of sensation. Such a division not only accounts for all the observed facts and for the normal sensibility of certain parts of the body such as the glans penis, but is also in accord with our knowledge of the evolution of the nervous system.

Hitherto I have put forward mainly clinical observations in support of this division of sensation, but in this paper I wish to refer also to corroboration which has been obtained by research in comparative anatomy.

The clinical support for the conclusion that there are two distinct systems has been submitted more fully in other papers (3, 5), and it is only necessary to summarise it briefly here.

(1) After division of a peripheral nerve of any size, a definite dissociation is demonstrable in what is termed the intermediate zone. In this region certain elements of sensation are lost and certain others retained: the former are concerned with the discriminative aspects of sensation and the latter with the protective.

(2) Occasionally it happens, after division of a peripheral nerve, as in the triangle in Head's experiment, and invariably after section of the posterior roots of spinal nerves, that a complementary type of dissociation is encountered. Such a dissociation is in every way the reverse of that found normally in the intermediate zone after division of a peripheral nerve, the protective system being lost and the discriminative retained. The occurrence of exactly complementary areas of dissociated sensation definitely indicates

the existence in cutaneous sensibility of two systems, which are independent and not simply concerned with the modification of the same fibres and end organs.

(3) During recovery after suture of a peripheral nerve, both cutaneous and deep sensibility recover in two distinct stages. The first stage is concerned with the recovery of the protective elements of sensation and the second with the discriminative. If the part be cooled, during the final period of recovery, it is found that the discriminative elements of sensation disappear and the accompaniments of the first stage return, demonstrating again the relations of the two systems of elements, and the probability of such features as over-action being release phenomena.

(4) In a number of cases of suture of peripheral nerves very incomplete recovery of sensation occurs. In an appreciable percentage recovery does not proceed beyond the first stage, yet in such patients the condition and peculiarities of the first stage persist *indefinitely*. This persistence seems to eliminate the possibility that the characteristic features of the first stage of recovery are due to such hypothetical states as incomplete repair of nerve fibres or end organs, or to irritation.

(5) Studies of the normal sensibility of the glans penis have shown conclusively that it is only endowed with the protective forms of sensation, and exhibits the same characteristics and peculiarities (excluding reference) as are seen at the end of the first stage of recovery after suture of a nerve. These observations must again prevent us from alleging that the first stage (or System I) has a pathological explanation. Any conception of sensation submitted must be capable of explaining the normal sensibility of the glans penis, and, as far as I can determine, the two systems conception is the only one yet put forward which does this.

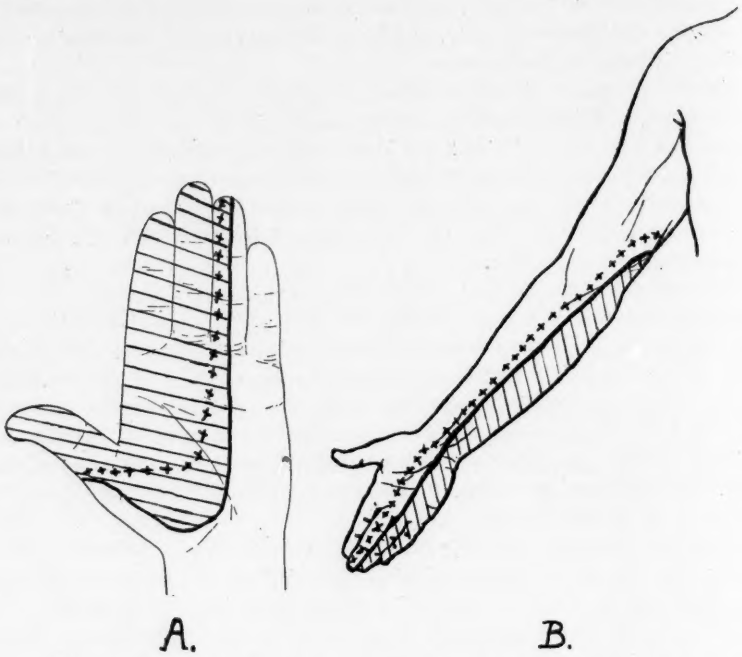
While the clinical evidence in favour of the dual nature of sensation appears to be most formidable and convincing, there is to be found in addition considerable support for such a conclusion in comparative anatomy: in fact, some workers (as Parsons (6)) find greater support in comparative anatomy than in the observations upon the human subject. Two pieces of evidence from such a source will be mentioned briefly, as they have been so fully dealt with by Parsons and more recently by Woollard (7), but I wish to submit a third which, as far as I am aware, has not been previously presented.

(1) In the lowest vertebrates the cutaneous receptors are of the simple free-ending type. In the Amphibia there are a few Pacinian corpuscles, but it is not until we reach the reptiles that the more complicated receptors occur in any number, and even in them the free endings are more numerous. It is suggested that the simpler receptors are connected with the more primitive protective system, and the more complicated ones with the discriminative system. In support of this it must be stated that there is some reason for the belief that even in man the noci-receptors are of the free-ending type.

(2) Studies of the functions of the sensory paths in the spinal cord have shown that

(*a*) the fibres concerned fundamentally with protective functions soon cross in the cord, and extend in a cephalic direction in the posterior spino-thalamic tract of the opposite side;

(*b*) those concerned with the discriminative aspects of sensation ascend throughout, or for considerable distances in, the posterior column of the same side.



To show the complementary types of dissociation of sensation found after (A) division of a peripheral nerve and (B) division of posterior roots. The cutaneous extent of the loss of the protective elements is shown by crosses and that for the discriminative elements by a continuous line.

Researches in comparative anatomy have demonstrated most definitely that the spino-thalamic tract is phylogenetically older than the tracts of Goll and Burdach. There is no doubt about the great age of the fibres which decussate in the cord, owing to the demonstration of their existence in Fishes and Amphibia by Edinger, and the proof of their presence throughout the whole vertebrate series that has been established by numerous observers. The evidence of the more recent evolution of the sensory fibres in the posterior columns is equally convincing, and has been clearly presented by Brouwer (8).

He has shown that there is no definite evidence of posterior column nuclei until we reach the reptiles. In a study of the relative size of the posterior columns compared with the whole extent of the white matter, he has proved that, when certain allowances are made for special functions and character of the epidermis, there is evidence of a progressive increase in the relative size and importance of the posterior columns. This progressive increase is particularly obvious in Mammalia, the higher mammals exhibiting relatively much larger posterior columns than those seen at any other vertebrate level. The maximum relative development is found in man. Brouwer and his co-workers have also shown that ontogenetically the posterior columns develop later than the sensory pathway, which crosses in the cord.

(3) It has been well known for a long time that the dissociation of sensation seen after division of nerve roots differs from that observed after section of a peripheral nerve in one of the limbs, but the significance of this observation does not appear to have been fully appreciated.

After division of a peripheral nerve, using Head's terminology, the loss of epicritic sensibility is greater than the protopathic loss, i.e. the intermediate zone exhibits the presence of the latter and the absence of the former. Following section of posterior roots, the part which is analgesic to a pin prick and unresponsive to the extremes of temperature is consistently greater in size than the portion of skin manifesting an absence of epicritic sensibility—i.e. the intermediate zone exhibits the presence of epicritic sensibility and the absence of protopathic. Investigations have further shown that there is very little overlapping of the epicritic, but considerable of the protopathic fields, after section of peripheral nerves of the limbs. Following division of roots, on the other hand, the overlapping of protopathic fields is quite insignificant.

These observations have led to the belief that a peripheral nerve may be regarded as the unit of epicritic sensibility, and a posterior root as the unit of protopathic supply. With reference to this, it is of importance to remember, first, that originally all the spinal nerves had a segmental distribution and the brachial and lumbo-sacral plexuses were evolved later; and secondly, that it has been shown that protopathic sensibility is concerned with protection, the more primitive functions of sensation, and epicritic sensibility with the more recently acquired discriminative faculties. This infers that the protective elements in cutaneous sensation have a segmental distribution, whilst the discriminative follow the arrangement of the peripheral nerves.

Recalling the history of the innervation of the limbs, the complementary dissociation of sensation observed after section of peripheral nerves or roots can be well understood, if the discriminative (cortical) system has been superimposed upon the protective (thalamic) system at a later date. If this interpretation, which appears to be the only reasonable one, is correct, we are presented with another important piece of evidence supporting the division of sensation into two systems. It is one which is in harmony with all the clinical observations and also with the other evidence advanced by researches

in comparative anatomy. In fact the more deeply we probe into the mysteries of sensation the more emphatically and distinctly are the older protective and more recent discriminative systems revealed to us.

SUMMARY

The evidence from examination of the human subject, and from comparative anatomy, in support of the division of sensation into two systems—protective or thalamic, and discriminative or cortical—is reviewed.

The significance of the complementary dissociation of sensation observed after division of peripheral nerves and roots is discussed.

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THE LYMPHATIC DRAINAGE OF THE HUMAN HEART

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I. INTRODUCTION

(1) General

In recent years the lymphatic glands of the mediastinum in their relation to disease have been a centre of interest for many observers. The physician, pathologist and radiologist have all contributed to the compilation of an extensive literature, a great share of which has been concerned with the relationship between lymphatic glands of the mediastinum and tuberculous disease.

The writings of Anthon Ghon (1) in Germany, and of Canti (2) in England, alike stress the value to the study of pathology of an exact knowledge of the inter-relation of a lymphatic gland and its drainage area.

Canti showed that from inspection of diseased lymph glands in the mediastinum it was possible to anticipate the position of a tuberculous lesion in the lung. Not only was it possible to predict that the right or the left lung was the seat of disease, but, further, the lobe of the lung could be indicated by gland inspection. Such knowledge as this, by narrowing the field of search, evidently brings invaluable aid to the pathologist when he is searching for a restricted lesion, possibly minute in size.

Canti and Ghon, using this method, are both enabled independently to arrive at the most important conclusion, namely, that in children, the primary site of tuberculous infection of the lymph glands of the mediastinum is to be found in the lung.

Up to the present, the lymph drainage of the heart has not been determined with the same degree of exactitude.

Standard works on Anatomy could not enable a pathologist, after demonstrating infective disease of the heart, to turn to the glands of the mediastinum and demonstrate those which drain the heart.

Conversely, the pathologist, again relying on the information to be gleaned from standard works on Anatomy, could not be led to suspect that disease were located in the heart from examination of lymphatic glands only.

While it may be that some pathologists customarily associate certain glands with the lymph drainage from the heart, it is certain that this association is the outcome of their extended experience, and not of information derived from works on Anatomy. No text-book of anatomy to which I have access contains precise information on this topic.

The acquisition of any precision in the knowledge of the method of lymph drainage from the heart to the glands of the mediastinum becomes especially urgent for two reasons.

First, because for some years the attention of many observers has been focussed on problems of heart disease, and particularly on that of rheumatic infection of the heart.

Secondly, because, as will be shown later, there is a close relationship between those glands receiving lymph drainage from the heart, and those receiving lymph from the lung. In fact, it may be categorically stated, certain glands near the right lung root receive lymph from both sources, heart and lung.

It is proposed to put forward in this paper:

(1) A brief review of the present state of knowledge, as to the paths of lymph outflow from the heart and as to the lymph glands of their destination.

(2) To contribute certain original observations, in amplification of existing accounts of the lymph drainage system of the heart, in order to give anatomical precision to a description both of the vessels by which lymph leaves the heart and of the glands in which they terminate.

It is felt that such a description is an essential first step in compiling a complete account of the lymphatic system of the heart, which should naturally include the intimate lymphatic channels of the myocardium, of the valves and of the auriculo-ventricular bundle.

(2) Present Knowledge of the Lymphatic Vessels of the Heart

I have selected for discussion three of the leading text-books on human anatomy, viz. those of Gray, Morris and Piersol; also two special works on the lymphatic system, viz. those of Poirier, Cuneo and Delamere and of Paul Bartels.

All these authors agree that there are present in the human being two main lymphatic trunks which convey lymph from the heart. These lymph trunks, it is stated, are formed in the coronary or auriculo-ventricular sulcus from tributaries which, broadly speaking, arise—one system from the right auricle and right ventricle, and the other from the left auricle and left ventricle.

The nomenclature, in most of these accounts, corresponds with the drainage areas; the lymph trunks are named right and left, according as they drain the two right or the two left chambers of the heart. Morris and Bartels describe a relationship of the origins of the right and left trunks to the origins of the right and left coronary arteries.

Regarding the anatomical relations of the trunks distal to their points of origin, the descriptions are meagre and often in obvious disagreement.

The Right Lymphatic Trunk. Of the right lymphatic trunk, *Gray's Anatomy* (3) states "it ascends in the posterior longitudinal sulcus and then runs forwards in the coronary sulcus and passes up behind the pulmonary artery...."

Piersol (4), alone of the authors I have consulted, fails to differentiate between the anatomical position of the right and of the left lymphatic trunks. He describes two trunks, but gives a name to neither. The vessel, which as far as I can discern corresponds with the right trunk of other authors, is stated to ascend "along the posterior surface of the pulmonary aorta."

Piersol and Gray evidently agree in the opinion that there is a relationship between the right lymphatic trunk and the posterior aspect of the pulmonary artery.

In Morris' *Anatomy* (5) an account is found in which a relationship between the right lymphatic trunk and the aorta is described. Thus: "The right stem accompanies the right coronary artery to its origin, passes over the arch of the aorta...." Bartels (6) gives the same account in almost the same words. In both accounts an anterior direction and destination for the lymphatic trunk is implied.

These two views, of Gray and Piersol on the one hand, and of Morris and Bartels on the other, are irreconcilable the one with the other, though study of the text makes it clear that the drainage areas of the lymph trunks described in the two accounts are the same. Poirier, Cuneo and Delamere (7), after having described the origin of the right trunk in the right portion of the auriculo-ventricular groove, and its position definitely on the anterior surface of the heart, state "it then ascends between the pulmonary artery and the aorta."

This account is not irreconcilable with that of Morris and of Bartels; indeed it supplements their account, lending some precision by the statement that the trunk lies between the aorta and (presumably the front of) the pulmonary artery.

In brief, two opinions prevail; one that the right trunk lies behind the pulmonary artery, the other that the trunk lies on the front of the aorta, between it and the pulmonary artery.

The Left Lymphatic Trunk. A similar divergence of statements is found regarding the position of the left lymphatic trunk. Again, a statement of relationship with the posterior aspect of the pulmonary artery is found, but now the statement refers to the left lymphatic trunk.

Gray writes: "A single trunk ascends between the pulmonary artery and the left atrium." Such a relation to the pulmonary artery can only be posterior.

Poirier, on this occasion in support of Gray, writes of the left trunk that "it runs between the left auricle and the pulmonary artery"; evidently a posterior position with respect to the pulmonary artery is suggested.

Bartels modifies this account when he states that the left trunk proceeds backwards and outwards below the pulmonary artery, and then under the aortic arch; and, as I infer from the context, turning forward to do so. Morris merely states that the trunk "passes behind the arch of the aorta" to a destination which I presume to be anterior.

Discussion

Piersol's account is the most difficult to follow: he alone fails to describe two lymphatic trunks with different critical relations. I am partly reminded by Piersol's description of the arrangement of lymphatic trunks found in the rabbit, which I have described elsewhere—see section (5) *Previous Research.*

It seems likely that Bartels and Morris have drawn upon a common source for their information; indeed Cruikshank is named by Bartels. The similarity of the accounts of these two writers, both as to statement and as to diction, is striking. Morris' description of the left lymphatic trunk given above does not really represent a different opinion, it is a curtailed version of the same account as Bartels uses. Unfortunately I have had no opportunity of consulting the writings of Cruikshank.

From a survey of the descriptions, given by the writers I have quoted, of the positions of the two main lymphatic trunks that leave the heart, we may draw the following conclusions.

(1) Two trunks only are described, viz.:

(*a*) A trunk in intimate relationship with the posterior surface of the pulmonary artery. This trunk is associated with the right drainage area by Gray, and with the left drainage area by Piersol, Poirier, Bartels and Morris.

(*b*) A trunk on the front of the aorta, lying also probably in intimate relationship with the pulmonary artery (Poirier). Morris, Bartels and Poirier associate this trunk with the right lymphatic drainage area.

As will be shown later, these descriptions correspond approximately to those of the main lymphatic trunks of the heart.

(2) A confusion has arisen in connecting the lymph trunks with their respective drainage areas. Some writers have connected the right drainage area with one trunk, and others the left drainage area with the same trunk, and conversely.

(3) Present Knowledge as to the Lymph Glands which receive the Lymph Outflow from the Heart

None of the authors I have consulted describes more than one destination for the lymph outflow from the heart. As will appear later, glands in two entirely different and distinct positions function as receivers of lymph from the heart.

From examination of the literature it appears that two, or perhaps three different opinions are current as to the position of the lymphatic glands which receive the drainage from the heart.

The following groups are described by different authors:

(1) *The Anterior Mediastinal Glands.* This nomenclature receives the support of Morris and of Bartels.

(2) *Tracheo-bronchial Glands.* This is a term of somewhat vague meaning, whose value will be discussed later.

It seems from examination of the figures of the various authors that the term "tracheo-bronchial glands" may cover either of the following:

(*a*) Glands above the lung root, lying in the superior tracheo-bronchial angle, i.e. the superior tracheo-glands,

or (*b*) Glands in the inter-bronchial angle or bifurcation of the trachea, inferior to both bronchi, i.e. the inferior tracheo-bronchial glands.

Piersol, together with Poirier, Cuneo and Delamere, supports the latter view, namely, that the inferior tracheo-bronchial glands are the receivers of lymph from the heart. Gray leaves it uncertain, both in the description in the text and in the figure, to which of these two gland groups the lymph drainage is directed.

(4) Nomenclature of the Lymphatic Glands of the Mediastinum

Before embarking on a description of the lymphatic system of the heart, it is necessary to discuss, in a little detail, the terminology most suited to the lymphatic glands of the mediastinum.

The writings I have referred to above contain different names for the lymphatic glands which lie in close relation to the great air passages and to the lungs.

Thus Poirier, Cuneo and Delamere describe and figure a group of glands lying in the angle between the two bronchi, below the trachea, as the inter-tracheo-bronchial glands, using the terminology of Baréty.

The term "bronchial nodes," used by Piersol, is vague; but it seems from the figure (p. 967) that the author refers by this name to these glands in the inferior inter-bronchial angle.

The annotation of fig. 776 in *Gray's Anatomy* leaves it quite uncertain whether by "tracheo-bronchial glands" the author intends to indicate the gland group in the tracheo-bronchial angle, above the lung root, or the group in the inferior inter-bronchial angle, below the trachea.

The conflicting accounts of the lymph drainage system of the heart, given by these and other authors, and discussed above, are the more difficult to understand because of the vagueness and the variance of their respective terminologies.

I have tabulated the different terms used in descriptive writings by the several authors whose views I have quoted. At the head of each vertical column is the name of the author; each horizontal column contains what, after close study of the descriptions, I have been led to regard as equivalents. In the sixth column is a brief anatomical note, and in the seventh the nomenclature which was used by Canti, and which I intend to follow strictly in this paper for the following reasons.

Table showing the homologies between the various nomenclatures of the lymph glands of the tracheo-bronchial system

Poirier after Barety	Bartels after Waldeyer	Morris	Gray	Piersol	Description	Proposed terminology
Peri-tracheo bronchial glands	Lymphoglandulae bronchiales	Bronchial nodes	Tracheo-bronchial lymph glands	Bronchial nodes	Descriptive name of the glands draining lungs trachea and bronchi	Tracheo-bronchial lymph glands
	Lgl. para-tracheales	Tracheal nodes	Para-tracheal glands		Glands by the side of the trachea	Para-tracheal glands
Prae-tracheo-bronchial glands R. and L.	Lgl. tracheo-bronchiales dextrae et sinistrae	Tracheo-bronchial nodes R. and L.	Tracheo-bronchial R. and L.	Tracheal nodes	Glands in the angle between the trachea and bronchus	Superior tracheo-bronchial glands R. and L.
Inter-tracheo-bronchial	Lgl. bifurcationis	Inferior tracheo-bronchial		Bronchial nodes proper	Glands in the inferior inter-bronchial angle	Inferior tracheo-bronchial glands
Inter-bronchial glands	Broncho-pulmonary glands	Pulmonary glands	Broncho-pulmonary glands Pulmonary glands	Pulmonary nodes	Glands in the angles of division of the bronchi in lung root Glands in the angles of division of the bronchi in the lung substance	Broncho-pulmonary glands

A more recent paper by Canti (8) includes a nomenclature at once anatomically accurate and reduced to such a degree of simplicity as has not been achieved by other writers. Further, in a locality where detailed precision is difficult, this simple nomenclature has been proved to provide a precision sufficiently accurate for writing pathological records.

Scott and Beattie (9), in a recent paper, insist that the glands of the mediastinum should be subdivided into the two groups, mediastinal and tracheo-bronchial. The second are those glands in intimate relation with the lungs and great air passages. In their description, fortunately, these authors follow

Canti. For the mediastinal glands, i.e. those glands in positions other than that of being intimately related to the great air passages, the anatomical subdivisions of the mediastinum into superior, anterior, middle and posterior may suffice.

I do not propose to discuss the different terminologies of the glands of the lung roots, shown in the fifth horizontal line of the table. These glands are outside any present application to my purpose, and are only included to complete the table.

The data attributed to *Gray's Anatomy* are taken for the purposes of the table from the figure on p. 776. In the text the contributor refers, in the briefest terms only, to tracheal, bronchial, broncho-pulmonary and pulmonary subdivisions of the whole tracheo-bronchial system of lymph glands.

(5) Previous Research

In the *Journal of Anatomy*, vol. LXII, Jan. 1928, I published a preliminary account of the lymphatic drainage of the mammalian heart. This paper contained the results of an introductory investigation of the lymphatic drainage of the hearts of the rabbit and the sheep. Information as to the arrangement in the rabbit was obtained by a correlation of the results (*a*) of indian ink injection into the heart during life, with (*b*) a study of the lymphatic gland groups involved by infection after an experimentally produced endocarditis in rabbits by means of pathogenic bacteria.

The results were unexpected and striking in their simplicity of demonstration. The main lymph outflow of the rabbit's heart is by two vessels which converge to a gland which lies just outside the pericardium, between the right superior vena cava and the arch of the aorta, and in front of the right pulmonary artery. This gland I provisionally designated the "caval gland" of the heart.

Jamieson and Dobson's prussian blue suspension was used for making injections into the sub-serous tissues of the sheeps' hearts. In this animal two types of lymphatic arrangement were found. In the first, two trunks, anterior and posterior, converged to the neighbourhood of the superior vena cava. In the second, an anterior trunk only was directed to the region of the superior vena cava; the posterior was led to the back of the left auricle.

The destination of these two trunks in the sheep was not positively determined in either type.

For details of the arrangements in the rabbit and sheep, the reader is referred to my earlier paper.

A very few preliminary notes of post-mortem room findings in cases of infective endocarditis suggested that the lymph drainage of the human heart combined certain features characteristic of both sheep and rabbit.

A gland corresponding to the "caval gland" was found in a few instances. A gland on the back of the left auricle (extrapericardial) was also found in

more than one instance. For this latter gland I provisionally suggested the name "auricular gland" of the heart.

(6) Objects of this Research

Enough has been said to show that there is still great uncertainty concerning both the position of the lymph glands which drain the heart, and also the anatomical sites occupied by the lymphatic efferent vessels of the organ.

The objects of this research were:

(1) To define the anatomical situations of the lymph efferent vessels of the human heart.

(2) To localise the lymphatic glands to which the efferent lymph vessels of the human heart drain.

II. MATERIAL AND METHODS

Hearts of male Bantu natives, unaffected by disease, secured in the post-mortem room and seldom more than 24 hours after death, were used. Care was taken to leave the bulk of the mediastinum, including the lymphatic glands, in position.

On reaching the laboratory the specimens were washed free of surface blood and clot in the chambers by immersion in cold water.

Injections of prussian blue suspension, prepared after the method of Jamieson and Dobson (10), were made into the subserous tissues. Injections were made with an ordinary Record syringe and a fine hypodermic needle. Injection was started systematically in each case near the apex of the left ventricle. Fresh successive stabs were made, working towards the coronary sulcus both on the front and the back of the heart, at intervals of about $\frac{3}{4}$ or $\frac{1}{2}$ in.

Frequently the injected material accumulated in patches of about $\frac{1}{2}$ in. diameter, before flow through the lymphatic vessels was observed. Frequently, on the other hand, an injection was more fortunate and a lymphatic vessel was pierced at once, in which case the fluid would flow instantly for an amazing distance, even to the actual glands of drainage. A little light massage often assisted the entry of prussian blue into a lymph vessel in more obstinate cases. By inadvertence, venous radicles were also sometimes injected. Light stroking of a vessel in its length towards the coronary sulcus readily demonstrated when such an accident had occurred. A vein, under this treatment, is very easily emptied of its colour; a lymphatic vessel, on the contrary, always retains its colour. Further, a vein is thick walled, and the colour of the fluid contained is thereby somewhat obscured.

The calibre of a vein, followed towards the coronary sulcus, increases perceptibly and rapidly. The calibre of a lymphatic vessel, on the contrary, does not appreciably increase in a distance of an inch or more. A lymph vessel,

indeed, may follow its course for the greater part of the length of the left ventricle without recognisable gain in macroscopic calibre.

After injection was completed, the hearts with adnexa were immersed in 5 per cent. formalin solution until firm enough for dissection, i.e. about a week.

Dissecting the finer lymphatic radicles, which are very fragile and thin walled, from the layer of subserous fat in which they are imbedded is a very tedious task. This, however, was carried out in order to ratify the findings by ocular demonstration. It was found preferable to dissect off the serous layer in one sheet before undertaking deeper dissection with the help of needles and a sharp eye-spud under a binocular magnifier.

The results of these procedures disclosed arrangements sufficiently regular to be regarded as portraying the normal arrangements of the lymphatic drainage of the heart of the Bantu native.

III. SYSTEMATIC DESCRIPTION

(1) The Superficial Lymphatic Vessels of the Heart

Two features of the superficial lymph vessels impress themselves on the observer from the earliest stages of the investigation.

(*a*) As has been stated above, the evenness of calibre of the smaller lymph vessels is noteworthy.

(*b*) Anastomoses between the fine vessels on the surface of the heart are very numerous. A fine meshwork of vessels is the result of successful injection of an area.

The superficial lymphatic vessels discharge into larger vessels which group themselves into two systems around the origins of the two coronary arteries.

The writers I have quoted earlier, with the exception of Poirier, Cuneo and Delamere (of whose terminology more hereafter) and Piersol have all designated these systems right and left. These designations are legitimate, being derived from a broad consideration of the drainage areas.

I prefer to designate these systems anterior and posterior, because these terms seem to me more descriptive, not only of the positions of the main lymph collecting trunks, but also because they are applicable to the position of the glands into which they drain. The drainage areas of the right and of the left trunks are not, in my experience, capable of exact demarcation, and since this is the case, the main reason for their nomenclature falls away. Attempts to demonstrate the lymphatic vessels draining the auricles have been, in the main, unsuccessful. The difference of texture and the rugosity of the external surface of these chambers, as compared with the ventricles, have combined to make a technique, already difficult, consistently unsatisfactory.

On one occasion lymphatic vessels were traced from the appendix of the left auricle to the nearest, the posterior, collecting trunk. I think it may be

assumed that the auricles drain into the two main collecting trunks. Accordingly, I have not included a systematic description of the lymphatic drainage of the auricles in the following notes.

The following drainage areas on the surfaces of the ventricles can, however, be broadly recognised.

(*a*) *The drainage area of the anterior collecting trunk* is limited to the right ventricle and the conus arteriosus. It may be stated that the whole surface of the right ventricle does not drain only to the anterior collecting trunk. The posterior collecting trunk claims a small share in the drainage of a portion of this ventricle, as will shortly be pointed out.

(*b*) *The drainage area of the posterior collecting trunk includes* the whole of the surface of the left ventricle and a narrow strip of the right ventricle immediately to the right of the anterior interventricular groove. In this groove lie two or three prominent longitudinal lymph vessels that convey lymph finally to the posterior collecting trunk. A narrow strip of the surface of the right ventricle adjacent to the posterior interventricular groove is sometimes found to drain to the posterior trunk and sometimes to the anterior trunk.

(2) The Anterior Cardiac Lymph Collecting Trunk (*truncus lymphaticus cordis* anterior)

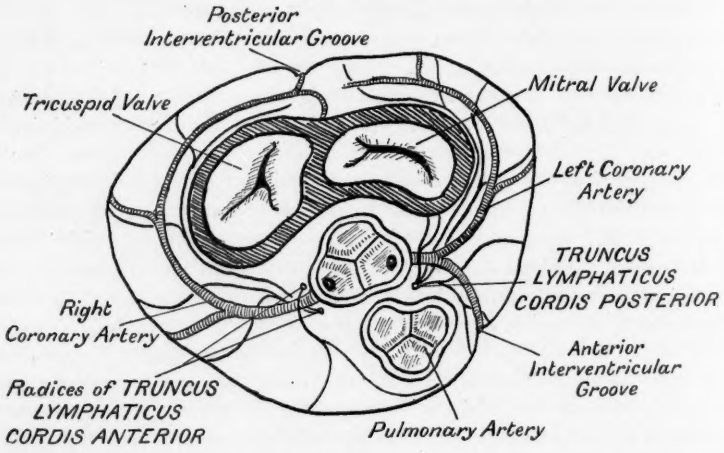

Fig. 1. This figure represents, in a schematic fashion, the mode of formation of the two lymph collecting trunks. The heart is looked upon from above, the auricles, the aorta and the pulmonary artery have been cut away.

The origins of the coronary arteries are shown with the main tributaries of the anterior and posterior collecting trunks forming plexuses around them.

Note the general position of the larger vessels is between the coronary arteries and the auriculo-ventricular junction both on the right and the left side.

In this scheme, a vessel joining the plexus around the left coronary artery from the left auricle is represented. The branch from the conus arteriosus to the plexus round the right coronary artery is also shown.

Fig. 1 shows in schematic fashion the plexus of lymphatic vessels around the origin of the right coronary artery that results from the confluence of lymphatic tributaries to that region.

The smaller lymph tributaries appear to be distributed with frequent anastomoses over the surface of the right ventricle, in a somewhat irregular network, but the larger vessels into which they drain tend to run parallel with the long axis of the heart.

One of the main tributaries arises on the under flattened surface of the heart, to the right of the posterior interventricular groove, and follows a semicircular course forward in the right coronary sulcus. This tributary, shown in fig. 1, receives finer radicles which join it at intervals along its course approximately at right angles.

Other vessels from the margo acutus and the anterior curved surface of the right ventricle come to lie also in the right coronary sulcus. One vessel, apparently very constant, from the front of the conus arteriosus crosses the right coronary artery superiorly and joins the plexus.

In general, the vessels in the right coronary sulcus, with the exception of the last mentioned, tend to lie deep to the right coronary artery, i.e. nearer the auricular-ventricular junction.

From the plexus of lymph vessels around the right coronary artery emerges the anterior cardiac lymph collecting trunk.

Relation of the anterior cardiac lymph collecting trunk to the serous and fibrous pericardium

Fig. 2 shows the course of the anterior cardiac lymph collecting trunk after emergence from the coronary sulcus. This vessel runs upwards along the front of the aorta under its serous covering, lying in close relation to the cleft between the aorta and the pulmonary artery. This relation tallies with Poirier's account of the so-called right collecting trunk.

During these dissections I have found that, at the level of the summit of the pulmonary artery, i.e. the inner arch of the aorta, or a little higher, occur changes in the relation of the serous and of the fibrous pericardium.

The serous membrane, which lower down invested the heart and then enveloped the aorta and the pulmonary artery, is now reflected from these vessels over the inner surface of the fibrous pericardium in order to form the parietal layer of the serous pericardium.

In fig. 2 an anterior view of the heart is shown. The anterior surface of the heart is bare of serous membrane, and a vertical strip of the same membrane has been removed from the anterior aortic-pulmonary junction, in order to display the anterior cardiac lymph collecting trunk. The cut edge of serous membrane is shown in a heavy continuous black line. The remnants of the fibrous pericardium, after the lower part has been removed, is shown also in fig. 2 with its cut edge distinguished by cross-hatching. From this structure

also a vertical strip, corresponding to that taken from the serous membrane, has been taken.

It will be seen that the fibrous pericardium, after losing its inner serous investment, blends with the fibro-areolar adventitia of the aorta, and with the adventitia which invests the great arterial trunks, arising from the arch of the aorta and also the superior vena cava and its tributaries. In the region

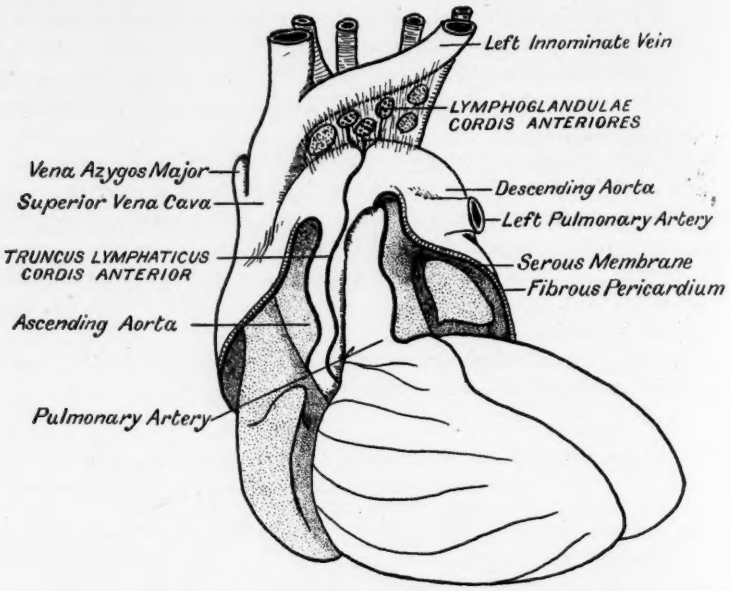

Fig. 2. This figure, drawn from dissected specimens, shows the position and termination of the truncus lymphaticus cordis anterior. The heart, with the remnants of the pericardium, the superior vena cava and the arch of the aorta, is viewed from the front.

The serous membrane has been removed from the surface of the ventricles and a vertical strip taken from the aortic-pulmonary junction. The fibrous pericardium has been removed with the exception of the upper part which blends with the adventitia of the great vessels. A strip of fibrous pericardium, corresponding to the aortic-pulmonary junction, has also been removed from the arch of the aorta in the mid-line.

The cut edge of the fibrous pericardium is indicated by a double line with cross-hatching, and that of the serous membrane by a heavy black line.

of the great vessels the fibrous pericardium is soon lost as a distinct layer. Consequently, at the level of the summit of the pulmonary artery, or a little higher, the anterior lymph collecting trunk parts company with the serous pericardium. The upward course of the vessel is continued in the fibro-areolar tissues which link the fibrous pericardium to the adventitial sheaths of the great vessels.

The anterior cardiac lymph collecting trunk terminates in the fibro-areolar

tissue of the superior mediastinum by discharging into a small group of lymphatic glands that lie in the same tissue just below the left innominate vein. A short distance below its termination the vessel commonly divides into three branches which enter respectively three of the medially situated glands of the group.

Apparently three or four only of the glands of this group, those more medially situated, receive the anterior cardiac lymph trunk or its branches.

(3) The Glands of Destination of the Anterior Cardiac Lymph Collecting Trunk (*lymphoglandulae cordis anteriores*)

A group of small lymphatic glands lies just below the left innominate vein, in the mid-line of the body very near to the point where the two pleural membranes come into contact.

This group contains as a rule five or six members disposed in a situation roughly parallel and inferior to the vein.

The anatomical relations of this gland group may be summarised thus:

Superior. The left innominate vein.

Anterior. The thymus gland.

(*Note.* In natives of South Africa the remains of the thymus are usually to be found in this position. From my post-mortem room experience I am under the impression that this gland in the Bantu peoples is of greater extent and persistence than in the European. The comparative anatomy of the thymus gland, however, has not been included in the scope of the present enquiry.)

Lateral. The reflection of the pleura from the mediastinum to the anterior wall of the chest. This relation, though essentially the same on both sides, is rather more intimate on the left side.

Posterior. The summit of the aortic arch, rather inferiorly, and the origins of the innominate and left common carotid arteries. The left vagus nerve descending along the inner side of the left common carotid artery I have found about $\frac{1}{2}$ in. posterior to the glands.

These glands should certainly be considered mediastinal, and in accordance with a strict terminology—superior mediastinal.

In examining a number of dissections of the mediastinum, I have noted that the anatomy of this region varies in the following respects:

(1) The level at which the left innominate vein crosses the mid-line may vary. In some cases the vein is lower and lies anterior to the aortic arch, in other cases the vein is superior to the aortic arch and in front of the origins of the great arterial trunks. In the first case the extrapericardial course of the anterior lymph collecting trunk must be very short, if the relation of the glands to vein as described is a constant one. I have not met the condition in connection with any heart I have injected with prussian blue, and consequently am not able to state what change takes place if the left innominate vein occupies a low position. I have, however, always found glands below

the left innominate vein, whether the vessel occupies the low or the high position.

In the example I have described and figured, the left innominate vein occupies a high position.

(2) The fibrous pericardium, and the reflection of serous membrane from it to the aorta and pulmonary artery, may occupy a higher position. In transverse, i.e. horizontal, sections I have found the superior cul-de-sac of the pericardial cavity in a posterior relation to the left innominate vein. In this case the anterior lymph glands, I should expect, lie immediately outside the pericardium.

(4) The Posterior Cardiac Lymph Collecting Trunk (*truncus lymphaticus cordis posterior*)

Fig. 1 shows that the general arrangement of the tributaries is similar to that of the anterior lymph collecting trunk. Proceeding towards the coronary sulcus, in a direction approximately parallel with the long axis of the heart, many lymph tributaries join a semi-circular vessel that begins near the posterior interventricular groove and lies in the left coronary sulcus. Certain other vessels ascend from the margo obtusus and the sloping front of the left ventricle to follow a course in the left coronary sulcus with the first.

As fig. 1 shows, these vessels lie in the left coronary sulcus closer to the auriculo-ventricular junction than does the left coronary artery.

In the neighbourhood of the origin of the left coronary artery these vessels are joined by others which have ascended on the anterior aspect of the left ventricle parallel with the anterior interventricular groove. Two or three conspicuous vessels ascend in or near the anterior interventricular groove. The resulting formation constitutes a plexus around the origin of the left coronary artery. From this plexus the posterior cardiac lymph collecting trunk arises. At first this trunk lies in the cleft between the aorta and the pulmonary artery, as fig. 3 shows. In its upward course the trunk comes to lie on the posterior aspect of the pulmonary artery. This relation has been described by certain authors, as we have seen in the Introduction (2), but the further course of the trunk has not apparently received attention.

As far upwards as the bifurcation of the artery, the posterior collecting trunk lies in the tissue between the pulmonary artery and that layer of serous membrane that forms the anterior wall of the sinus transversus.

Fig. 3 shows the left posterior aspect of a heart from which the auricles had been removed in order to display the anterior wall of the sinus transversus. The line of attachment of the fibrous pericardium to the adventitia of the divided pulmonary artery is shown. The cut edge of the fibrous pericardium is represented here by cross-hatching. A vertical strip of serous membrane has been removed from the posterior aortic-pulmonary junction to show the posterior cardiac lymph collecting trunk, and the surface of the left ventricle

is also bare of serous membrane. The cut edge of serous membrane is represented by a heavy black line.

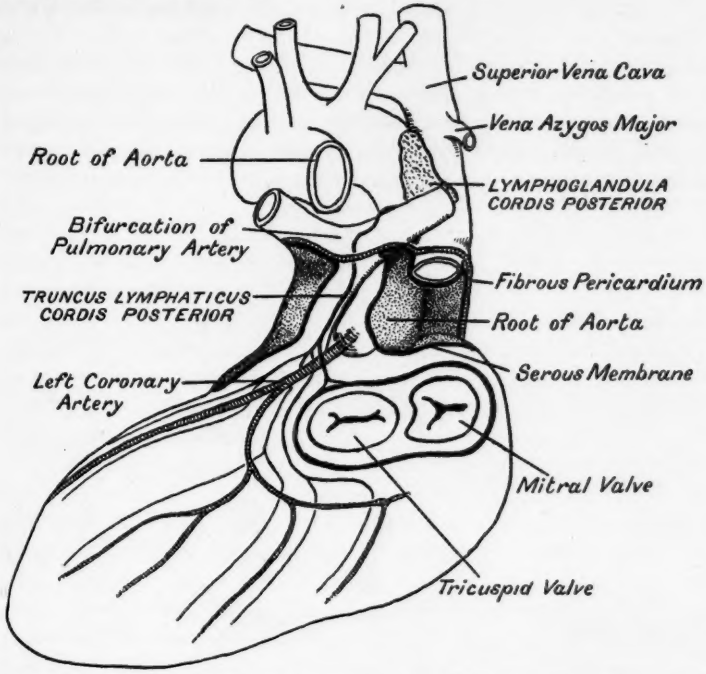

Fig. 3. This figure, drawn from dissected specimens, shows the formation and position of the truncus lymphaticus cordis posterior. The heart is viewed from a left posterior aspect after the auricles have been cut away from the ventricles and the superior vena cava. The anterior wall and floor of the sinus transversus are exposed by this procedure. On the posterior surface of the aorta and the pulmonary artery the cut edge of the fibrous pericardium is represented by a double line and cross-hatching.

A strip of serous membrane has been removed from the aortic-pulmonary junction to display the truncus lymphaticus cordis posterior. The cut edge is represented by a heavy black line. The surface of the left ventricle is also bare of serous membrane.

Extrapericardial course of the posterior collecting trunk

The upper surfaces of the right and left pulmonary arteries lie outside the pericardium. The fibrous pericardium blends with the adventitial sheaths of the two branches of the pulmonary artery. Traced forwards and upwards from the front of the pulmonary arteries, the fibrous pericardium blends with the ligamentum arteriosum and with the sheaths of the aorta and the superior vena cava.

The serous membrane at the level of the bifurcation of the pulmonary artery is reflected backwards from the aorta and the pulmonary artery, which

it has invested up to this level in order to form the roof and posterior wall of the sinus transversus. Fig. 4 shows the extrapericardial course of the posterior lymph collecting trunk in a posterior view of the heart and pericardium.

At about the level of the bifurcation of the pulmonary artery the lymph trunk parts from the serous membrane, which lower down invested the aorta and the pulmonary artery, and enters the fibro-areolar tissue that envelopes the pulmonary artery. Above the bifurcation the lymph trunk, lying in the adventitial sheath of the pulmonary artery, turns to the right upon the posterior aspect of the right pulmonary artery.

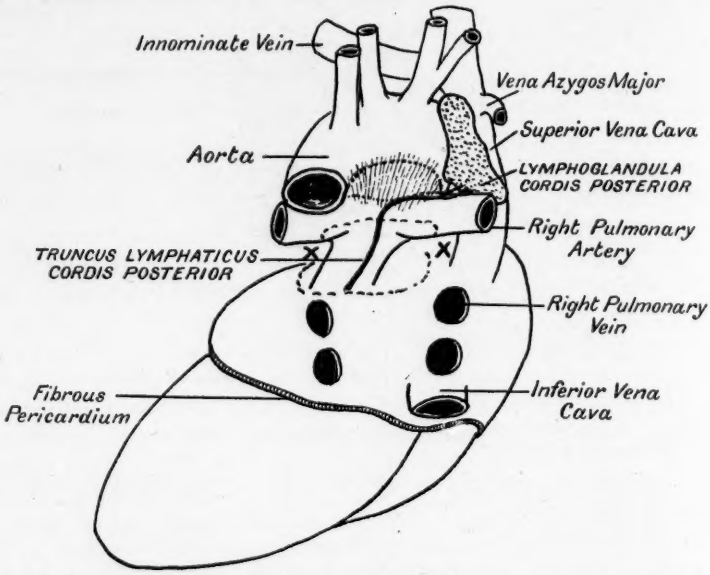

Fig. 4. This figure demonstrates in a posterior view of the heart the terminal part of the course of the truncus lymphaticus cordis posterior. This vessel is seen on the posterior aspect of the pulmonary artery in the region of its bifurcation.

The dotted line *XX* represents the lines of union of the fibrous pericardium with the adventitia of the pulmonary artery. A partial separation has been made between these two structures and part of the intrapericardial course of the lymph trunk is also shown.

The lymphoglandula cordis posterior lies posterior to the angle between the superior vena cava and the ascending aorta and immediately above the right pulmonary artery.

In its course upwards and to the right, the lymph trunk comes to lie on the superior surface of the right pulmonary artery, and finally enters a lymph gland which lies above the right bronchus and above the right pulmonary artery, behind the angle between the superior vena cava and the ascending aorta. This gland (lymphoglandula cordis posterior) is the lowest member of the right superior tracheo-bronchial group.

The position of the proximal part of the posterior lymph collecting trunk

was indicated by several authors, but no indication of the actual site of termination or of the asymmetrical course of the vessel was afforded by any writings available to me.

(5) The Glands of Destination of the Posterior Cardiac Lymph Collecting Trunk (*lymphoglandula cordis posterior*)

There is usually a large mass of glandular tissue above the right lung root, the lower end of which receives the posterior cardiac lymph trunk. This glandular mass shows only the slightest indication, by a slight constriction, that there may be a morphological separation of the lower part from the upper. I have always found that the lower part cannot actually be separated from the upper without cutting through gland substance (see fig. 4).

From my injections and dissections, it seems that the lymphatic drainage of the heart is to the lower part only of this glandular mass. It is possible that the quantity of fluid introduced into the lymphatic system by my technique was insufficient to colour the whole mass, and that, despite the above suggestion, the entire mass does participate in the drainage of the heart.

This, at least, is certain: the stain received by the posterior trunk is collected first by the lower part of the gland mass under consideration, and does not diffuse equally or readily through the whole mass.

The termination of the posterior cardiac lymph collecting trunk may, therefore, be stated to be the lowest member of the right superior tracheo-bronchial group.

The anatomical relations of this gland may be summarised thus:

Superior. The main mass of the right superior tracheo-bronchial gland group.

Inferior. The right pulmonary artery: the right bronchus is rather posterior than inferior (see fig. 5).

Medial. The right tracheo-bronchial angle.

Lateral. The right lung, separated from the gland, in part, by the vena azygos major, and, in part, by broncho-pulmonary lymph glands.

Anterior. The aorta and the superior vena cava to the left and the right front respectively. Inferiorly lies that part of the pericardium that links the right pulmonary artery to the sheaths of the aorta and the superior vena cava.

This gland is to be regarded as homologous with the "caval" gland of the heart, demonstrated in the rabbit and previously described. The prominent relations of both the lymphoglandula cordis posterior and the caval gland of the rabbit's heart present the following points of similarity:

(1) In each case the gland is right sided and extrapericardial in position.

(2) The anterior relations are the aorta and the superior vena cava. The superior vena cava in man corresponds to the right superior vena cava of the rabbit, in which this vessel is duplicated.

(3) An intimate relation to the right pulmonary artery is found in both cases. In man this vessel is inferior, but in the rabbit posterior.

The lymphoglandula cordis posterior is unlike the caval gland of the rabbit in this respect; in man this gland receives the lymph conveyed by the posterior collecting trunk only; in the rabbit the caval gland receives the whole lymph

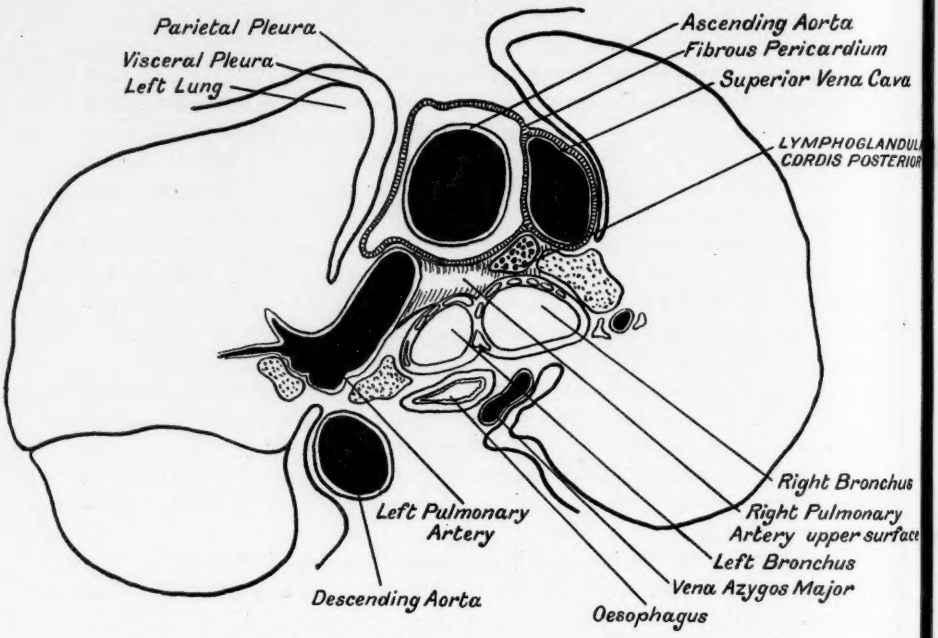

Fig. 5. This figure is a reproduction of a tracing of a horizontal section made through the lymphoglandula cordis posterior.

The pleura is represented by a heavy black line, which defines the two lungs and the mediastinum between them.

In front are shown the ascending aorta and superior vena cava, enclosed by the fibrous pericardium, which is seen at this level to blend with the sheath of the superior vena cava.

Behind these two vessels and outside the pericardium lies the lymphoglandula cordis posterior, distinguished from other lymph glands by heavy dotting. Below the gland is shown the upper surface of the right pulmonary artery.

The section passes just below the bifurcation of the trachea, and the right bronchus is shown posterior to the lymphoglandula cordis posterior. The vena azygos major crosses the lung root to join the superior vena cava at a level about $\frac{1}{4}$ in. higher.

drainage of the heart. Two trunks drain to the caval gland in the rabbit, and lie in the closest apposition to each other on the under side of the pulmonary artery. They cross to the right side below the bifurcation, and not above the right branch as in man.

IV. VARIATIONS

The lymph drainage system of the human heart, as already described, consists of anterior and posterior collecting trunks together with their tributaries. The terminations of these trunks are, first, the medial members of the lymph glands which lie below the left innominate vein, and, in the second place, the lower members of the right superior tracheo-bronchial glands. I have observed no substantial variation from this system in any of the human Bantu hearts which I have examined. Certain variations in the details of the collecting trunks have, however, been observed and are described below.

Collecting Trunks

Usually the anterior collecting trunk has been found represented by a single vessel, but on occasions by several vessels running in company. The same statement applies to the posterior collecting trunk. A tendency for the terminal vessels to unite, separate and reassemble is noticeable. I have met with a tripartite condition of the anterior and of the posterior collecting trunks with about equal frequency. The anatomical relations, however, of the main collecting trunks as described above are very constant.

Interpolated Lymph Glands

I have observed, on occasions, what I am assured is a matter of some importance, namely, small lymphatic glands interpolated between the points of formation and of termination of the lymph collecting trunks. Such interpolated glands seem more common

(*a*) on the posterior collecting trunk,

(*b*) on a trunk which has broken up for a space into a plexus, though they have been found also interrupting a single main collecting trunk.

Examples of interpolated lymph glands are given below arranged in two groups according as they occurred on the intra- or the extrapericardial part of the course of a collecting trunk.

Bartels (11), under the name "lymphoglandulae cordis propriae," refers to two small lymph glands found by various observers on the surface of the heart.

A "Lgl. sub-epicardialis praeaortica," it is stated, sometimes occurs on the front of the aorta in a half-moon shaped fatty fold of epicardium, and can be displayed by injection of the "right heart wall."

A "Lgl. sub-epicardialis juxta-pulmonalis" also may be found, sometimes in association with the other, on the left side of the pulmonary artery in a vertical fatty fold of epicardium.

I have not encountered these glands, but suggest that a gland interpolated on the anterior or posterior trunk might correspond to Bartels' description of Lgl. sub-epicardialis praeaortica or juxta-pulmonalis.

Intrapericardial Interpolated Lymph Glands

Examples. (1) A gland measuring 10 mm. and 4 mm. in its long and transverse diameters occurred in the length of the posterior trunk, just at the upper end of its intrapericardial course.

(2) A gland measuring 4 mm. and 2 mm. in its long and transverse diameters was found on the middle portion of a tripartite posterior trunk in the middle of its course.

(3) A gland measuring 3 mm. and 2 mm. in its long and transverse diameters interrupted one of the main tributaries of the posterior collecting trunk, in the left coronary sulcus.

(4) A gland measuring 4 mm. by 8 mm. lay at the base of the right auricular appendix on the front of the right auricle in the right coronary sulcus. This gland interrupted a tributary of the anterior collecting trunk.

Extrapericardial Interpolated Lymph Glands

I have noted a single example.

A small gland was found on the middle portion of a tripartite termination to the posterior collecting trunk. The gland lay midway between the bifurcation of the pulmonary artery and the gland in which the trunk terminated.

V. SUMMARY AND CONCLUSIONS

In the rabbit the lymph gland of drainage of the heart lies on the right side immediately outside the pericardium, in close relation to the ascending aorta, the right superior vena cava and the right pulmonary artery. The lymph is conveyed to this destination by two lymphatic trunks which lie on the surface of the heart.

In the sheep's heart an anterior lymphatic trunk leads to the region of the superior vena cava, and a posterior trunk is also present. This posterior trunk at times takes a course to the region of the superior vena cava converging on the anterior trunk. At other times, the posterior trunk takes an independent course on the back of the pericardium in close relationship with the left pulmonary veins.

The arrangement of the lymph drainage of the rabbit's heart, combined with that of the second type found in the sheep, together with post-mortem observations on European hearts, the subject of infective endocarditis, led me previously to surmise that the lymph drainage of the human heart led to glands arranged as follows:

(1) Outside the pericardium, in a position defined by the ascending aorta, superior vena cava and right pulmonary artery, as in the rabbit (i.e. the so-called "caval" gland of the heart).

(2) On the back of the pericardium close to the left pulmonary veins, in a position corresponding closely to that suggested by one of the alternative

arrangements of the sheep's heart (i.e. the so-called "auricular gland of the heart").

The Lymph Glands of the Human Heart

We have seen that in the Bantu heart the lymph drains into two entirely different extrapericardial groups of glands, namely:

(1) The lowest of the right superior tracheo-bronchial glands, i.e. the caval gland of the heart.

(2) The medial members of a small group of lymph glands which lie in the mid-line of the body just below the left innominate vein. Previous enquiries had afforded me no information concerning the share of this gland group in the lymph drainage of the human heart.

My speculation as to the existence of an auricular gland has received no support; at least, in Bantus.

In the literature three different gland groups have been regarded as receivers of lymph from the heart.

(1) Poirier, Cuneo and Delamere, as well as Piersol, assign the lymph drainage to a group of glands lying in the inferior inter-bronchial angle, the inferior tracheo-bronchial glands. I have found no support for this suggestion.

(2) Morris and Bartels hold the opinion that the heart drains to anterior mediastinal glands.

(3) Gray refers the drainage to tracheo-bronchial glands, but unspecified as to position.

The last two views are independently false, but collectively true if we allow for looseness in the use of the term "anterior mediastinal," and for vagueness in the term "tracheo-bronchial."

The lymph drainage of the heart is constantly directed to two destinations:

(1) Glands of the tracheo-bronchial system.

(2) Glands to which the name "anterior mediastinal" might be applied with only a little laxity in the use of terms.

While each of these lymph gland groups may have been indicated as destinations, no single author has stated that both groups constantly receive the heart's lymph drainage, and that each group is functionally distinct from the other in the matter of the district that it drains.

The Lymph Vessels of the Human Heart

(1) The lymph vessels draining the heart lie in the subserous layer of its investment. Two plexuses of vessels are formed in the coronary sulcus around the origins of the right and left coronary arteries respectively.

(2) Two lymph collecting trunks emerge from these plexuses; these I have designated anterior and posterior.

The authorities cited in the introduction have used the terms "right" and "left" in most cases. These terms are broadly descriptive of the drainage areas

of the collecting trunks. Thus the right trunk drains the right ventricle, and the left trunk the left ventricle.

I have referred to the confusion of drainage areas and of lymph trunks at some length in the introduction.

Right is equivalent to anterior, and left to posterior of my nomenclature.

By this procedure I have reversed the nomenclature of Poirier, Cuneo and Delamere. The trunk draining the right ventricle they have called right, or posterior; the trunk draining the left ventricle they have called left, or anterior. I have taken the step of reversing these terms "anterior" and "posterior," after due consideration, for these reasons:

(1) In the anterior aspect of the heart, the anterior trunk only is visible. It lies on the anterior surface of the aorta, and therefore "anterior" is more descriptive than the "posterior" used by Poirier, Cuneo and Delamere.

(2) The glands of termination of the anterior collecting trunk lie anterior to the great vessels of the mediastinum. Strictly, in anatomical terminology, these glands are not in the anterior, but in the superior mediastinum. The term "anterior" is accurate, however, as regards their relation to the great vessels.

(3) The posterior trunk lies on the posterior surface of the pulmonary artery. It is not visible from the posterior aspect of the heart before the auricles have been removed, and the anterior wall of the sinus transversus exposed from behind. After that procedure, the term "posterior" becomes evidently suitable.

(4) The lymph gland of drainage of the posterior trunk is plainly posterior with respect to the heart and great vessels. It lies posterior to both the aorta and the superior vena cava.

We may conclude that:

(1) The lymph drainage of most of the right ventricle is directed by an anterior lymph trunk (truncus lymphaticus cordis anterior) to an extrapericardial group of lymph glands that lie in the superior mediastinum in close relation to the left innominate vein (lymphoglandulae cordis anteriores).

(2) The lymph drainage of the left ventricle is directed by a posterior lymph trunk (truncus lymphaticus cordis posterior) to an extrapericardial gland (lymphoglandula cordis posterior), which is a member of the right superior tracheo-bronchial group and lies in close relation to the superior vena cava, the aorta and the right pulmonary artery.

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A CONTRIBUTION TO THE STUDY OF THE COMPARATIVE HISTOLOGY AND PHYSIOLOGY OF THE SPLEEN, WITH REFERENCE CHIEFLY TO ITS CELLULAR CONSTITUENTS

I. IN FISHES

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INTRODUCTION

A fairly extensive literature has grown up around the comparative histology and physiology of the spleen. The most comprehensive account is probably that of Whiting (89), who covers practically the entire vertebrate field, with the exclusion only of very low vertebrates such as the Cyclostomes. His account gives one an excellent general idea of the micro-anatomical structure of the spleen throughout the vertebrate series, but from the very vastness of the area covered it could not possibly be a really close and detailed study. Other observers have covered less ground with consequently greater thoroughness. Bannwarth (4), for example, made a very close study of the spleen of the cat. Similarly Mall (45, 46, 47) carried out a series of valuable researches on the spleen of the dog. A fairly detailed account of the literature as a whole may be found in the papers of Krumbhaar (32) and v. Skramlik (82).

As far as the spleen of Fishes is concerned, the most complete and systematic histological description is that of Phisalix (65), written in 1885. His account is not very satisfactory from a modern standpoint, in view of the considerable advances in knowledge and histological technique which have been made since then. He describes the cells of the blood as being either red or white, but makes no mention of what is now considered to be a fundamental subdivision of the white cells into granulocytes and non-granulocytes, not to mention the further grouping of the granulocytes in accordance with their affinities for acid and basic stains; Ehrlich's classical work on the various types of leucocyte had only been published a few years previously, in 1878 and 1879 (17, 18).

Many papers have been published concerning the anatomy and embryology of the spleen in various fishes, with numerous incidental observations on its histology (2, 12, 29, 33, 35–40, 43, 50, 52, 54, 57, 58, 59, 64, 67–70, 72, 73, 77). The most extensive work on the development of the spleen has been done by Laguesse, who also investigated in great detail the structure of the capsule and connective tissue framework in the spleen of Selachii (39, 40). Pouchet (72) in 1882

gave a good account of the "terminaisons vasculaires" or ellipsoids in the spleen of Selachii.

Concerning the physiology of the spleen in Fishes, both Whiting and Phisalix (*op. cit.*) make some references to it *en passant*. Phisalix (66) wrote in addition a brief note about the rôle of the spleen in the formation of red blood corpuscles in lower Vertebrates. Bizzozero and Torre (5) in 1883, investigating the process of erythrocytopoiesis in Fishes, make occasional references to the splenic cells, but like Phisalix they too seem to have known only one type of white cell. Drzewina and Pettit (16) investigated the physiological effects of splenectomy, and Pettit (62) noted the appearance of fusiform cells in the blood after removal of the spleen. Gueylard (23) and Miescher-Ruesch (53) investigated the changes occurring in the spleen of Fishes when transferred from fresh to salt water. Drzewina (15) in 1905 made a systematic histological study of the lymphoid tissue of Fishes, excluding the spleen; and to some of her findings reference will be made during the course of this paper. Hemmeter (26) in 1926 described the spleen of *Alopias vulpes*. Tait (85) in 1927 gave an interesting account of the spleen of the skate, with special reference to its vascular and reticular arrangements, and to an experimental investigation into the function of the splenic ellipsoids.

TECHNIQUE

The exclusive use of the routine histological method of examination, namely the preparation of sections (usually after embedding in paraffin), is open to very grave objection in an investigation of this kind. Apart from such factors such as shrinkage and distortion, a more serious source of error is introduced on account of the marked changes in staining reaction which may ensue. This is a grave defect in haematological work, especially where the Romanowsky stains are used, as with proper control the staining reaction with eosin constitutes the main criterion by which one usually decides whether a given cell contains haemoglobin or not (90). In this respect it is often difficult to know which step or steps in one's histological technique are responsible for certain tinctorial changes, so one can only judge any particular technique as a whole. After methyl alcohol, as used for example in Leishman's stain, the cytoplasm of both erythrocytes and granulocytes stains with eosin, but there is a very distinct and recognisable difference in tint between the two. After Zenker's fluid on the other hand this difference in staining reaction tends to disappear. In addition there is a further defect associated with the use of eosin. Not only does it stain cells which do not contain haemoglobin, but it often fails to stain those which do; young red cells, which on examination in the fresh condition may be definitely seen to contain haemoglobin, will nevertheless, as is well known, usually pick out the methylene blue in an eosin-methylene blue combination. Furthermore, as pointed out by Werzberg (88), the fixation technique itself may produce this inverted staining

reaction in the cytoplasm of the erythrocyte. Consequently, although the study of sections affords valuable information, it may be very misleading unless one's conclusions are checked by the examination of fresh and unstained cells. And even then a cell which contains only a small quantity of haemoglobin may be difficult to distinguish from one which contains none at all. Okajima's specific stain for haemoglobin (60), it may be mentioned, did not give good results.

Any work on splenic cytology which relies only on sections loses a large part of its value, for only in a fresh smear preparation can the various splenic cells be clearly identified. The ordinary splenic smear however is open to two objections. As a mechanical result of the act of smearing, portions of cell protoplasm may be drawn out into long processes, which may be very misleading if their origin is not clearly understood (fig. 1). Furthermore, the cells are scattered irregularly all over the slide, and their relationship to one another is thereby completely upset. In order to overcome these disadvantages the "anatomical smear" was devised. With a pair of forceps one takes hold of a piece of spleen, one end of which has been cut quite flat, and gently applies the cut end to a glass slide, instead of smearing it along the slide in the usual manner. In fact the preparation is really a stamp, not a smear. The result is that the cells are transferred to the slide in the same relative position to one another as they occur in the cut end of the organ, and one really has the equivalent, as far as the loose cells are concerned, of a section of the organ one cell layer in thickness (fig. 2). That at least is the ideal aimed at in the preparation. In actual practice however the anatomical smear is not uniform, for in some parts two or three layers of cells may be deposited on the slide, and only in parts is the ideal of one cell layer attained. But where this occurs the preparation is extremely valuable, for one not only sees the splenic cells uncut and undistorted, but also in their exact natural relationship to one another. It may be observed that two precautions are necessary in order to make a good anatomical smear. First, the organ must be drained of all excess blood, otherwise blood exudes from the cut surface and spoils the preparation. In the present work the removal of blood was effected as a matter of routine, for the animals were all killed by cutting off their heads and allowing the blood to drain away from the cut end, exsanguinating in this way the entire body, including the spleen. In the second place the cut end of organ must be perfectly flat, and to secure this a sharp scalpel, or better still an ordinary safety-razor blade, is necessary.

For an understanding of the spleen one must also have some knowledge of the functionally associated tissues. To understand what cells the spleen contributes to the blood, one must be acquainted with the cell content of normal blood, and with the other organs concerned in haemopoiesis. According to Giglio-Tos (21) haemopoietic "lymphoid" tissue occurs in the lamprey in the spiral valve of the intestine. In many Teleosts also, though not in any of the Elasmobranchs examined, haemopoiesis occurs in the

"lymphoid" tissue of the kidneys (fig. 3), and in other scattered "lymphoid" deposits of which Drzewina (15) has made a very careful study. The thymus also (80) may be concerned in blood formation.

The spleen was examined in paraffin sections, cut at 3–5 μ, after fixation in Helly's modification (25) of Zenker's fluid, which preserves the granules of the granulocytes. In many cases the spleen was washed out with normal saline until the returning fluid was perfectly clear, and then perfused with the fixative. The entire organ was then immersed in the fixative for one hour, after which it was cut into thin slices and fixation and subsequent treatment carried out in the usual way. This technique, as will be shown later, gives a beautiful demonstration of the pulp reticulum and the pulp spaces. Frozen sections of spleen were also made, after fixation in 10 per cent. formol (made with filtered fresh sea water), for the examination of fats and lipoids. Smear preparations were made of every spleen, and were first fixed in formol vapour for 10 seconds, the slide being held over a 40 per cent. solution of formalin at a distance of 1·0 cm., being then treated after exposure to the air for a few hours with Leishman's stain. Some form of preliminary vapour fixation is absolutely essential to obtain well-fixed preparations of blood films and splenic smears in Fishes. Werzberg (*loc. cit.*) and Rawitz (74) also mention the trouble they experienced in securing good fixation. Two or three films were made from the blood of every animal, and also sections of liver, kidney and swim-bladder occasionally, when the naked-eye appearances seemed to suggest haemopoiesis.

Frozen sections, having been made chiefly for the study of fats and lipoids, were stained with Scharlach R and Sudan III. Paraffin sections were stained with haematoxylin and eosin, haematoxylin and Van Gieson's picro-fuchsin, Mallory's aniline blue connective tissue stain, Heidenhain's iron-haematoxylin, occasionally with orcein for the demonstration of elastic tissue, and with a modification of Leishman's stain which gave some of the most instructive results of all. The section is grossly overstained for one and a half to two hours with the ordinary Leishman's stain diluted with an equal volume of distilled water, and then differentiated with methylated spirits (about 95 per cent. methyl alcohol) and absolute alcohol, followed by xylol and neutral balsam. This technique was originally devised in order that both the sections and the smears might be treated with exactly the same staining reagents (Leishman having first of all been found the best stain for the smears), and so any differences in the staining reactions of the various cells, on comparing the smear with the section, would be due to differences in fixation and other treatment, and not to the stain used. In this way one was enabled to compare the various techniques in so far as they affected the staining reactions of the cells and tissues. It was found however that this modified stain was so excellent in other ways that it was retained long after its original purpose had been subserved.

EXPERIMENTAL WORK

In addition to the material obtained from normal animals, a series of Fish were subjected to experimental procedures. This experimental work was confined purely to the common dogfish, *Scylliorhinus canicula*. As a result of observations made on the spleen of the normal dogfish, certain conclusions were arrived at concerning the mechanism of blood formation which it was desired to confirm by stimulating blood formation through the production of an experimental anaemia. This was done by withdrawing a known quantity of blood; after the lapse of varying intervals, the fish was killed, and its spleen and associated tissues examined in the manner already described.

There are in the dogfish no easily accessible superficial veins from which one can withdraw blood as in Mammals; but there are some superficial venous sinuses from which the withdrawal of blood seems at first sight an easy matter. These sinuses however are usually half empty, and the pressure of blood in them is very low. The systemic arterial blood pressure in the fish (i.e. in the post-branchial vessels) is only of the order of 7–10 mm. of mercury (6), owing to the fact that the blood does not pass from the heart to the systemic arteries direct, but must first of all traverse the branchial capillaries; as a result the pre-branchial pressure of about 45 mm. of mercury becomes greatly reduced. The venous pressure is almost invariably negative. Consequently it was found that the best and easiest method of obtaining blood was direct cardiac puncture, a procedure which is not followed by any ill effects, even when the heart is punctured ten or fifteen times.

The heart is reached in or very close to the mid-line, from the ventral surface, immediately anterior to the pectoral girdle. Actually in the mid-line itself the pectoral girdle has a small spur anteriorly, which can easily be felt through the skin, so that the needle can be inserted to the side of it. The needle is directed dorsally and caudally, and is best inserted first of all by itself, without the rest of the syringe. As soon as blood appears at the end of the needle, one knows that the heart has been reached, and the syringe is then attached. On the average 37 per cent. of the total blood was withdrawn, and in some cases over 50 per cent. The blood in Fishes constitutes only 2 per cent. of the total body weight (81) as opposed to 7–8 per cent. in Mammals. The procedure adopted was to weigh the fish immediately before the withdrawal of the blood, and withdraw where possible 1 c.c. of blood for every 100 gm. of body weight, thus giving a withdrawal of approximately 50 per cent. of the total blood volume. This would appear to be sufficient to stimulate fresh blood formation. (Exact details are given in the appended tables.)

Cardiac puncture cannot be performed unless the fish is first of all given a general anaesthetic. This is done very simply by placing the animal in a freshly made 2 per cent. solution of ether in sea water; the vessel containing the animal is covered over by a thick sheet of glass which is kept firmly

Table I

Some details of a series of 25 dogfishes in which experimental anaemia was produced. In each animal two sets of observations were made: (1) at the commencement of the experimental period, when blood was withdrawn by cardiac puncture; (2) at the close of the experimental period, when after a varying period, to allow for various stages in the degree of activity of the haemopoietic tissues, the animal was killed. In each case observations above are those at the commencement of the experiment, those below are at its termination. The first column gives the number of the fish, prefixed by the letters 2ES (Second Experimental Series), the second gives the times of commencement and termination of the experiment, the third the number of erythrocytes per cubic millimetre of blood at the two times, the fourth a similar count for the leucocytes, the fifth the amount of blood withdrawn (in c.c.), the sixth the weight of the fish in grammes, and the seventh the number and arrangement of the identification threads.

No. of fish	Duration of experiment	R.B.C.	W.B.C.	Amount of blood withdrawn c.c.	Weight of fish in gm.	Thread
2ES 1	12. vii. 28	123,000	15,000	1·5	425	W
	28. vii. 23				390	
2ES 2	12. vii. 28	105,000	17,500	3·5	450	B
	18. vii. 28					
2ES 3	13. vii. 28	193,000	20,000	5·5	870	WW
	10. viii. 28	151,000	23,000		820	
2ES 4	13. vii. 28	165,000	8,600	4·0	620	WB
	8. viii. 28	145,000	19,000		615	
2ES 5	13. vii. 28	159,000	42,000	2·5	660	BB
	13. viii. 28				690	
*2ES 6	14. vii. 28	333,000	45,300	6·0	620	BW
	3. viii. 28	229,000	24,000		575	
2ES 7	14. vii. 28	144,000	19,000	3·0	550	WWW
	31. vii. 28	155,000	23,000		620	
2ES 8	14. vii. 28	During the cardiac puncture the heart stopped beating altogether, and no blood was obtained. Recovered on return to tank				WWB
2ES 9	15. vii. 28	125,000	28,000	2·0	540	WBW
	6. viii. 28	124,000	13,500		565	
*2ES 10	15. vii. 28	176,000	39,000	6·5	800	WBB
	7. viii. 28	140,000	17,000		780	
*2ES 11	16. vii. 28	203,000	29,000	4·5	750	BBB
	13. viii. 28	141,000	9,300		730	
*2ES 12	16. vii. 28	270,000	39,000	6·0	740	BBW
	31. vii. 28	176,000	36,000		725	
2ES 13	16. vii. 28	181,000	42,000	7·5	745	BWB
	9. viii. 28	200,000	26,000		685	
*2ES 14	17. vii. 28	250,000	46,000	9·5	1075	BWW
	12. viii. 28	132,000	21,000		1085	
*2ES 15	17. vii. 28	306,000	45,000	7·5	865	WWWW
	6. viii. 28	103,000	14,000		885	
2ES 16	18. vii. 28	188,000	12,000	1·0 and 4·0	820	WWWB
	13. viii. 28	159,000	21,000		730	
2ES 17	18. vii. 28	151,000	9,900	2·0	460	WWBW
	26. vii. 28				440	
*2ES 18	19. vii. 28	249,000	41,000	6·5	840	WWBB
	30. vii. 28	165,000	25,500		810	
2ES 19	19. vii. 28			7·5	675	WBBB
	8. viii. 28	145,000	15,000		610	

TABLE I (*continued*)

No. of fish	Duration of experiment	R.B.C.	W.B.C.	Amount of blood withdrawn c.c.	Weight of fish in gm.	Thread
2ES 20	20. vii. 28	158,000	9,900	1·0 and 4·0	630	WBBW
	10. viii. 28	190,000	22,000		520	
*2 ES 21	21. vii. 28	226,000	40,000	6·0	685	WBWB
	12. viii. 28	114,000	29,000		665	
*2ES 22	21. vii. 28	204,000	33,000	8·0	895	WBWW
	26. vii. 28				810	
*2ES 23	22. vii. 28	241,000	31,000	6·0	630	BBBB
	13. viii. 28	139,000	20,000		580	
*2ES 24	23. vii. 28	220,000	45,000	7·0	690	BWWW
	8. viii. 28	144,000	29,000		615	
*2ES 25	25. vii. 28	183,000	31,000	8·5	875	BWWB
	13. viii. 28	120,000	15,000		880	

Nos. 1, 2, 5, 17 and 22 died in the tank; no blood counts were taken post-mortem.
Weight was gained by 5, 7, 14, 15 and 25.
Loss of weight was only slight in 4, 10, 11, 12, 17 and 21.

pressed down until the splashing ceases, and through which the progress of the anaesthesia can be watched. The first effect of the anaesthetic is a purely irritant one, the fish splashing violently and irregularly. As the ether begins to take effect, a true convulsive stage follows (corresponding presumably to the excitatory stage in human beings) towards the end of which the movements take the form of rhythmical side-to-side oscillation. Finally respiration ceases and the muscles become quite flaccid. The respiratory cessation however does not come on quite suddenly, but is preceded by a period of irregular and disorganised breathing, shown by twitching and tremor at the angles of the mouth. This tremor, it may be noted, is also the first sign of recovery from the anaesthetic. Anaesthesia is usually complete after five minutes—sometimes less, very rarely more. When anaesthesia is complete, the fish is taken out of the water, and after being weighed is placed upon a plain wooden board. Manipulative procedures may be carried out for about ten minutes, after which time as a rule twitching at the angles of the mouth shows that recovery is commencing, and the fish may then either be re-anaesthetised by placing it in the ether solution once more, or returned to its tank, where it will commence to breathe regularly again after about fifteen minutes. After twenty or thirty minutes it swims about apparently quite normally. Recovery may be expedited by the performance of artificial respiration, which is very simply done by drawing the fish to and fro in the tank, and so maintaining an artificial circulation of water through the gills. Although the anaesthesia thus induced lasts for about ten minutes, only three or four minutes are required as a rule for the actual withdrawal of blood and marking of the animal.

The marking of the fishes for subsequent identification offers several difficulties. The most practicable method was found to be by means of varying combinations of black and white silk threads, which were stitched on the fishes' backs immediately in front of the posterior dorsal fin. The threads are first of all soaked in paraffin wax, in order to make them more resistant to the action of the sea water, in which they may have to remain for several weeks.

One may here observe that the question which has so troubled anaesthetists whether, in death under anaesthesia, respiratory or circulatory failure comes first, admits of a very easy answer in the dogfish; the dissociation between the respiratory stoppage and the circulatory is very much longer than in higher Vertebrates, and the heart goes on beating for twenty minutes, and even more, after respiration has been completely suspended.

In order partly to confirm the account given by Tait(85) of the functions of the ellipsoids, and partly to see whether any light might be thrown on the mechanism by which lipoid particles are held in the wall of the ellipsoid, three dogfishes were given an injection of 10 c.c. of a 4 per cent. solution of Indian ink in sea water. In one case the injection was intra-muscular, and in the other two intra-peritoneal, and in each case the fish was killed three days after the injection. As in the previous experiments the fish were first of all anaesthetised.

The question of the precise relationship of the various Fish groups to one another in the evolutionary scale has not as yet been answered with certainty. The arrangement in this paper follows the account of Fish genealogy given by Kyle(34). Accordingly the Dipnoi will be described first, then the Elasmobranchii, and finally the Teleostomi, that being according to Kyle the order in which the main Fish groups have diverged from the ancestral tree. It is of interest to note that this arrangement had actually been decided upon to begin with, from examination of the spleens alone, before any reference had been made to descriptions of Fish biology.

THE SPLEEN IN THE DIPNOI. *CALAMOICHTHYS*

I have to thank Mr G. L. Purser, M.A., of Aberdeen University, for kindly lending me a piece of *Calamoichthys*' spleen. This unfortunately was the only specimen I was able to obtain of the spleen of the lung-fishes (their natural habitat being the tropics), but it is extremely interesting. It shows with almost diagrammatic clearness the essential elements of the spleen, and its circulatory mechanism, arranged in a more primitive manner than in any other spleen examined.

Running throughout the entire length of the organ are the artery and vein, placed side by side, and surrounded by a mass of "lymphoid" tissue. Surrounding the "lymphoid" tissue is the splenic pulp, covered by a thin capsule consisting of a single layer of cubical cells (fig. 4). The term "lym-

phoid," whose precise significance will be discussed later on, is throughout this paper used only provisionally.

When serial sections are examined it can be seen that at intervals the artery gives off branches which pass through the lymphoid tissue to enter the pulp; from the pulp the blood drains into the splenic vein, to reach which it has to pass a second time through the lymphoid tissue. The venules are much more numerous than the arterioles. The pulp consists of a cellular reticulum surrounding the lymphoid tissue; in the meshes of this reticulum is contained blood, and here also the splenic venules commence. It may be seen that the circulation is so designed that the blood flows (*a*) through the pulp reticulum, (*b*) around the lymphoid tissue. An important part of the splenic function is discharged by the formation in the lymphoid tissue of cells which enter the blood stream. Now there are only two ways in which this entry of lymphoid cells into the blood stream may be effected. In the first place they may pass through the walls of the arterioles and venules as they traverse the lymphoid tissue. There is however absolutely no histological evidence to support this, for the walls of the vessels as they pass through the lymphoid tissue, though thin, are quite complete; they show no signs of openings, nor anything to indicate the probability of openings being formed, to permit the passage of cells. The second and almost certain access is directly from the outer part of the lymphoid tissue to the blood which circulates around it in the pulp. The region therefore between the lymphoid tissue and the pulp is *the* site of cellular interchange between the lymphoid tissue and the blood, and will in future be referred to as the "boundary zone." In the boundary zone the blood as it passes through the splenic pulp sweeps away with it the outermost cells of the lymphoid tissue (fig. 4 *a*).

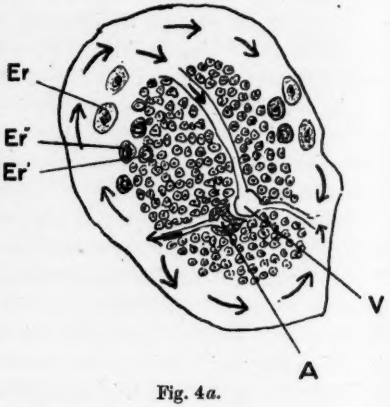


Fig. 4*a*.

It follows from what has already been said that in the boundary zone there is no sharp line of demarcation between the lymphoid tissue and the pulp; there is practically no connective tissue between the two, and the lymphoid tissue merges almost imperceptibly into the pulp, where the lymphoid cells may undergo certain phases of their development before entering the blood stream.

THE SPLEEN IN THE ELASMOBRANCHS

Of the cartilaginous Fishes there have been examined the common dogfish (*Scylliorhinus canicula*), the nursehound (*S. catulus*), the ray (*Raia clavata*), and the skate (*Raia batis*). For a detailed histological description the spleen of the dogfish has been chosen, for several reasons: it is the simplest to interpret, the dogfish is the most convenient animal for experimental work, and its cellular elements are large. The spleens of other fishes will be described only in so far as they differ from that of the dogfish.

SCYLLIORHINUS CANICULA

In contrast with the spleen of *Calamoichthys*, which has only two main elements—the lymphoid tissue and the pulp—the spleen of the dogfish has three essential constituents: (1) lymphoid tissue, (2) pulp, and (3) ellipsoids (fig. 5). The histological picture varies considerably according to the amount of blood which the organ contains. When the spleen is congested blood accumulates in the pulp, which consequently appears to be much more extensive than when the organ is first emptied of its blood, as happens when the fish is killed by cutting off its head and allowing all excess blood to drain away from the cut ends of the main vessels. Under such circumstances the pulp appears to diminish very considerably. What has happened is that the spongy reticulum, not having much blood in its meshes, undergoes almost total collapse. If however the spleen is perfused with normal saline, so as to wash out the last traces of blood, and then some fixative is run through, the pulp is prevented from collapsing, and its large-meshed spongy reticulum is beautifully shown (fig. 6). The capsule consists of a single layer of cubical cells with a thin stratum of connective tissue and a few elastic fibres underneath. Muscle elements are completely absent, and there is no trace whatever of a trabecular system.

The splenic arterioles terminate by dividing into three or four thick-walled capillaries, the ellipsoids, which then end by opening into the pulp spaces. The ellipsoids are really the splenic capillaries, differing from capillaries elsewhere merely in the greater thickness of their walls. The ellipsoids open directly into the spaces of the spongy pulp reticulum and commencing among the meshes of this reticulum are the splenic venules, which soon after their formation acquire a lymphoid sheath. Both arteries and veins therefore have a sheath of lymphoid tissue, as in *Calamoichthys*. Furthermore, it follows from what has just been said that the circulation through the splenic pulp is unquestionably an open one (figs. 6 and 7).

The ellipsoids practically never possess a complete lymphoid sheath, though often in contact with lymphoid tissue in part. They usually have a complete investment of pulp. Apart from the thickness of their walls the ellipsoids are also peculiar in that their lumen is usually very narrow, frequently to the verge of obliteration with a diameter of 5–6 μ, insufficient to

allow a red blood corpuscle to pass through without considerable compression and distortion. Hemmeter (26), examining the spleen of *Alopias vulpes*, appears not to have realised that the ellipsoids are blood vessels, but calls them "hemolytic islands." In contrast with the ellipsoids the lymphoid vessels have a larger lumen and permit of a much freer flow of blood.

Both the arteries and veins possess lymphoid sheaths, and so the communications of the lymphoid vessels vary accordingly. The arterioles lose their lymphoid sheaths and pass into the ellipsoids (fig. 8). The venules on the other hand, after their formation by the confluence of the pulp spaces, quickly acquire a coating of lymphoid tissue, and so this group of lymphoid vessels communicates directly with the pulp.

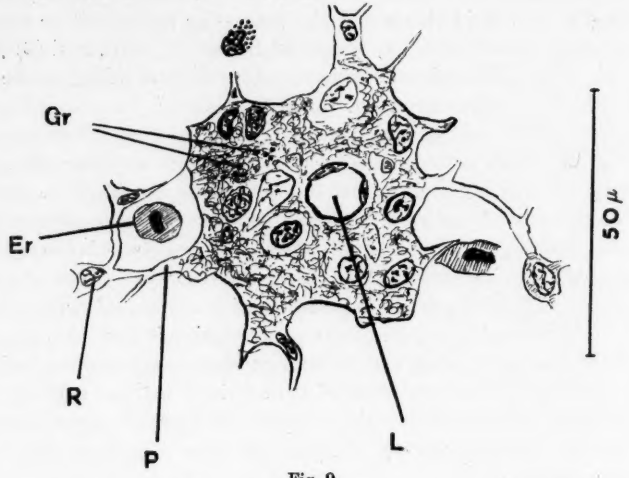


Fig. 9.

In an ordinary section (fig. 5) the wall of the ellipsoid is clearly and sharply defined, and on staining with Mallory or Van Gieson there is seen to be a condensation of connective tissue to form a thin but dense plate all round it. Nevertheless there are numerous processes extending from the wall of the ellipsoid into the pulp, where they become continuous with the processes of the pulp reticulum (figs. 7 and 9). These can be seen very clearly where the organ has been washed out with saline and then perfused with fixative.

The lymphoid tissue forms dense cellular areas which stain very deeply with nuclear stains. In the dogfish the lymphoid tissue is disposed in the form of a sheath around centrally placed blood vessels, and scattered among the lymphoid cells are large hyaline cells, with a cytoplasm which hardly stains at all with any of the stains used, and small pale often lobed nuclei. In general the term "lymphoid" appears to be used to denote any dense accumulation of small round cells, with relatively large nuclei and scanty

cytoplasm, bearing a superficial resemblance to the lymphoid tissue found in Mammals. Actually however there are very considerable differences between the lymphoid tissues of Fishes and Mammals, both in their component cells, and even more strikingly in the cells to which they give rise. In the dogfish for example the lymphoid tissue gives origin to all the cellular constituents of the blood, whereas in Mammals it has been believed until quite recently not to form any erythrocytes at all, and even of the white cells to produce only about one-third. In order however not to create any confusion by the introduction of new terms, the "lymphoid" tissue of Fishes will still be described as such, with the qualifications already mentioned.

Internally the lymphoid sheath is bounded by the wall of the vessel which is passing through it. The central lymphoid vessel varies in thickness according as to whether it is arterial or venous. The veins are very thin-walled. In paraffin sections, where there is very considerable tissue shrinkage, and the vessel wall appears in consequence to be even thinner than it really is, the impression is often produced that cells from the lymphoid tissue may enter the blood stream by passing through the thin vessel wall. In frozen sections however, where there is very much less shrinkage, it is obvious that the vessel wall is complete and uninterrupted, and that the small round cells do not enter the blood stream in this direct manner, but only obtain access to it indirectly by first of all entering the splenic pulp, and from there draining into the veins. It follows from this that externally the lymphoid tissue has no clear line of demarcation from the pulp; there is no connective tissue between the two, but the one merges imperceptibly into the other, so that it is impossible to say at what point the lymphoid tissue ends and the pulp begins.

The cells of the lymphoid tissue may be enumerated as follows:

1. *Small round cells.* These are the most numerous of all the cells to be found in the lymphoid sheath, and they stand out clearly by reason of their very scanty cytoplasm and the deep staining of their nuclei, which have well-marked limiting membranes and chromatin nodes. When seen in paraffin sections the small round cells vary very considerably in shape. In a splenic smear however they are all circular, and even more markedly than in the section they appear to consist almost entirely of nucleus, little or no peripheral cytoplasm being discernible. It is for this reason that French writers often refer to them not as cells, but as "Noyaux d'origine." In a smear preparation most of the nuclei are seen to be finely granular with a few larger chromatin nodules towards the centre. In those cells possessed of a cytoplasmic rim, the nucleus is usually finely reticulated.

2. *Large round cells.* These are about twice the size of the small round cells, and have more cytoplasm both relatively and absolutely. Their nuclei do not stain so deeply, the nuclear membrane, though well marked, is not so thick and dense, and the chromatin nodes are smaller and fewer than those of the small round cells. On the other hand a delicate intra-nuclear network is usually present. But although this description is applicable to a typical large round cell, there are so many intermediate forms between the large and the small round cell that there is no doubt the former arises by growth from the latter.

3. *Large hyaline cells.* These are very curious cells, and their occurrence is subject to very considerable variation not only in different spleens, but also in different parts of the same spleen. Owing to their large size they can be seen quite clearly under fairly low magnifications (×120) as clear rounded spaces, the cytoplasm taking up hardly any stain, with small central nuclei which are sometimes lobed, and stain as a rule very faintly (fig. 10). The hyaline cells are scattered irregularly throughout the lymphoid tissue.

4. *Cells undergoing karyo-kinesis.* These occur very infrequently in the normal spleen, and can only convincingly be demonstrated in those cases where the activity of the lymphoid tissue is experimentally stimulated. There is no collection of these mitotic cells to form a germ centre as described by Flemming in mammals (19). The dividing cells occur irregularly throughout the lymphoid tissue, tending to be rather more numerous near the central blood vessel, but not very markedly so.

5. *Granulocytes.* These occur mainly in the region of the boundary zone, in the outer portion of the lymphoid sheath. They are of two types, though in either case they are only the immature forms; for as soon as they approach maturity they leave the lymphoid tissue to enter the pulp and blood stream. One of the granulocytes I have ventured to call the "Perinucleate" cell, on account of the position of the nucleus, which is invariably situated at the periphery of the cell; and when the latter is seen in profile, the nucleus may be seen to be perched upon it. The nucleus is usually bilobed, but it may also be divided into three or four lobes, and so closely resemble the nucleus of the polymorpho-nuclear neutrophile leucocyte of higher vertebrates. The granules in its cytoplasm however are strongly eosinophilic. The perinucleate cell is about one and a half times the size of the small round cells, and its granules are spherical. In the second type of granulocyte on the other hand the granules are usually rod-shaped; in a smear preparation, more so in the ordinary than in the anatomical smear, the granules of both types of cell tend to be scattered all over the field. The nuclei of the neutrophiles are round or nearly so, never attaining the lobulation of the perinucleate nuclei, from which they also differ in being more centrally placed.

6. *Immature red cells.* Small round cells which are just commencing in the boundary zone to develop into erythrocytes, and then pass into the pulp.

Examination of the pulp in sections alone is very misleading. The length of an average red blood corpuscle is about 27 μ, and of the nucleus 10 μ, leaving about 8·5 μ of clear haemoglobin at either end of the cell. If through an erythrocyte of this size sections 3 μ in thickness are taken, there will be a maximum of ten sections altogether, only four of which will contain any of the nucleus, while in the other six sections portions of the haemoglobin-containing cytoplasm will be cut off without any nucleus. These will appear as seemingly isolated masses, which might be interpreted as fragments of haemoglobin from old broken-down erythrocytes, or alternatively as free haemoglobin accumulating for the formation of new erythrocytes; at any rate, whatever interpretation one were to put upon them, judging merely from the section one would come to the very paradoxical conclusion not only that there are present masses of free haemoglobin, but that they are nearly twice as numerous as the masses of nucleated haemoglobin, whereas actually they do not exist at all! It is therefore only in the smear that one gets any accurate conception of the true shape and appearance of the cellular constituents of

the spleen; and in a smear of the dogfish's spleen one sees at once that there are no fragments of free haemoglobin. With these preliminary remarks one may proceed to enumerate the cells of the pulp as follows:

1. *Reticulum cells.* The pulp proper consists of a loose cellular reticulum, in whose meshes are the free cells of the circulating blood. The spongy reticulum can collapse to a very small volume when emptied of blood, and on the other hand can open up considerably when the organ becomes congested, and so accommodate large quantities of blood. The reticulum establishes important connections with the smaller blood vessels. Processes of the reticulum cells are attached to the walls of the smaller splenic veins, which they help to strengthen. Laguesse(40) describes the reticulum cells as forming "cones of insertion" where they join the vein walls. This is not invariable, though quite frequent. The reticulum cells are also connected by numerous processes with the walls of the ellipsoids (fig. 9), as has already been mentioned. The cellular reticulum can only be clearly seen in those spleens which have been first of all washed out with normal saline to remove excess blood, and then perfused with the fixative. Any general stain will then serve to demonstrate the reticulum perfectly.

2. *Red blood corpuscles.* As seen in section these show extensive variation both in size and shape, but these variations are partly due to the well-known elasticity of the erythrocytes which allows them to be compressed into almost any shape, and partly to the fact that they are cut in different planes. Much more significant is the variation in the size and density of the nuclei of the red blood corpuscles. The nuclei of the adult erythrocytes in the general circulation are small and dense. In the splenic pulp however there also occur erythrocytes with nuclei which are larger and less dense in texture; between these and the mature erythrocyte with its small and more compact nucleus all types of intermediate cells are to be found, with nuclei diminishing in size and increasing in density until the appearance is reached of the mature nucleus of the circulating erythrocyte. Concurrently with the diminution in size of the nucleus, the haemoglobin content of the cell increases, so that there is roughly an inverse proportion between the two. When the cell is immature the nucleus is large and the haemoglobin scanty; as the cell becomes mature the nucleus becomes smaller and the haemoglobin more plentiful. Of especial interest is the fact that the younger erythrocytes, with large nuclei and scanty cytoplasm, are identical with the small round cells; and careful examination of the peripheral parts of the lymphoid sheaths reveals many small round cells which are just acquiring a narrow rim of haemoglobin. This process of the development of the small round cell into the erythrocyte can be seen to be going on even in the normal spleen, but the appearances are much more convincing and decisive in those cases where blood formation has been stimulated by the production of an experimental anaemia. Incidentally the fact that the nucleus of the adult erythrocyte is already a partially atrophic structure foreshadows the condition found in higher Vertebrates where the process of atrophy is carried to completion.

3. *Granulocytes, of both the eosinophile (perinucleate) and neutrophile variety.* The granulocytes occurring in the immediate vicinity of the lymphoid sheath, i.e. the boundary zone, are immature. Even more obviously than the young red cells, they are being formed from the small round cells by the acquisition of a narrow granular rim which gradually increases. At the same time the nucleus, at first perfectly spherical, becomes more irregular in shape and finally attains the lobulated condition which characterises the mature granulocyte (fig. 11, 1–13, and fig. 12).

The ellipsoids in paraffin sections present a finely granular and reticular appearance, the reticulation only showing up under high magnification

(× 600 +). In the meshes of this reticulum small granules of brownish pigment may be seen occasionally, and now and again a red blood corpuscle. The presence of erythrocytes in the walls of the ellipsoids is shown much more clearly in the spleen of the ray, and also in many Teleosts. There are several nuclei in the ellipsoidal wall, and as definite cell boundaries are usually absent, it would appear to be syncytial in nature. The red blood corpuscles in the ellipsoidal wall are obviously undergoing haemolysis, and it was this no doubt which led Hemmeter(26) to describe the ellipsoids as "hemolytic islands" without perceiving their relation to the blood vessels.

A fact which has not been mentioned by previous observers is the frequent appearance in the ellipsoid wall of considerable quantities of lipoid granules. In a frozen section of dogfish's spleen it can be seen that these granules accumulate mostly in the outer part of the ellipsoid wall, and here and there they may be seen passing into the pulp (fig. 13). This fact would appear to be of considerable significance in connection with the physiology of the ellipsoid.

The physiology of the dogfish's spleen.

From the histological appearances which have just been described it is possible to arrive at certain conclusions concerning the physiology of the dogfish's spleen. Blood entering the spleen passes through lymphoid tissue, through an ellipsoid, and so enters the pulp (figs. 7 and 8). During its passage through the ellipsoid it is exposed to considerable resistance owing to the great narrowing of the lumen, and in consequence of the increased resistance its rate of flow is very much reduced. Presumably the more fragile corpuscles become broken down, and those which are not fragile already tend to become so. The red cells as a whole, or the fragments resulting from their disintegration, are ingested by the phagocytic cells in the wall of the ellipsoid, where they undergo complete breakdown. Presumably their degeneration products are in part the source of the pigment granules which one sees in the ellipsoid wall, and in part, though this cannot be seen, pass into the pulp where they are employed in the formation of fresh red cells. It is highly probable that the breaking down erythrocytes in the ellipsoidal wall undergo some fatty change; this would account for the presence of the lipoid particles. Certainly it seems more feasible to assume that the breakdown of the erythrocyte is the source of this lipoid accumulation, than to assign to it some function altogether apart from the haemopoietic system, in connection with the general metabolism of fats and lipoids.

Tait(85) in some recent experiments showed that Indian ink particles injected into the blood stream rapidly disappeared from the circulation, and were then to be found in large quantities in the walls of the ellipsoids. This finding of Tait's was confirmed in the present experimental work, details of whose technique have already been given. "In fishes just as in mammals the sessile phagocytic cells of the ellipsoids capture foreign particles introduced into the blood stream, and probably also ingest effete corpuscular

elements of the blood" (Tait). Tait only observed with certainty the ingestion of Indian ink particles. It is in addition undoubtedly true that in most Fishes the ellipsoidal phagocytes ingest corpuscular elements in the form of erythrocytes, but not granulocytes.

During the passage of the blood through the pulp, it comes into contact with the outer part of the lymphoid sheath, and in this boundary zone cellular interchanges take place. Between the pulp and the lymphoid sheath there is practically complete absence of connective tissue, so that the cells can move about quite freely. The mere fact that connective tissue is so completely lacking at the boundary between two such cellular tissues as the pulp and the lymphoid sheath would in itself, merely from the structural point of view and quite apart from all other considerations, strongly suggest that there are occurring cell migrations with which the presence of connective tissue would interfere. From the lymphoid tissue cells are continually entering the pulp, from which they pass into the general circulation. The small and large round cells may either enter the blood as such, and then presumably circulate unchanged, although it is quite possible that even after they have entered the blood they may undergo further differentiation; or they may remain for a while *in situ*, and undergo the first stages of their development into erythrocytes or granulocytes, entering the blood stream to complete only the final phases of their development. The lymphoid tissue therefore gives rise to all the cellular elements of the blood, and is the fundamental haemopoietic tissue. In the ellipsoids on the other hand there would seem to be a mechanism for blood destruction.

A point of interest in connection with the maturation of the erythrocytes in the dogfish is that a large part of it occurs in the blood stream itself. In the blood of a normal dogfish one may constantly see many immature red cells. They can easily be picked out by reason of the fact that their cytoplasm contains less haemoglobin than the mature cell, and their nucleus is larger and much less dense. They become much more numerous when erythrocytopoiesis becomes more active, as in the present experimental series.

RAIA CLAVATA AND *RAIA BATIS*

Both the common or thornback ray (*Raia clavata*) and the skate (*Raia batis*) belong to the same fish group as the dogfish, and the essential features of their spleens are very similar. The capsule is rather thicker, and consists of several layers of fibrous tissue covered by a thin layer of flattened epithelium. The ellipsoids are thinner than those of the dogfish, having an average diameter of about 60 μ. They show even more clearly than in the dogfish a definitely reticulated and granular appearance, and the presence of red blood corpuscles in their wall, in varying degrees of dissolution, may be very frequently observed (fig. 14). The pulp is more extensive than in the dogfish, and its cellular reticulum is more dense. Tait (*loc. cit.*) observes that

"the lymphoid tissue is not an essential element in the structure of the spleen." This is a statement with which the histological findings in the present work are not in agreement. Lymphoid tissue is of universal occurrence in all the spleens examined, and is as "essential" an element in the structure of the spleen as any other, if it is not in fact the most essential in the spleen of Fishes, from the point of view of haemopoiesis.

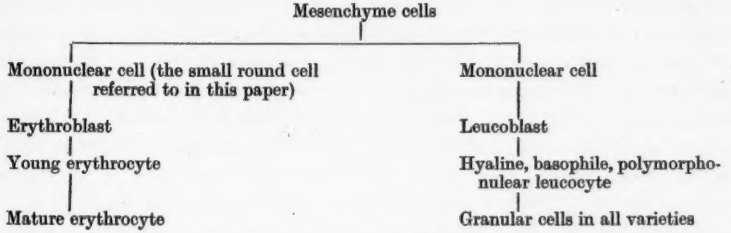
The cells in the spleens of the ray and skate are, broadly speaking, the same as those of the dogfish. The eosinophile leucocyte has very large granules which are only loosely attached to the cell, and which are set free in large numbers when one makes a smear or a blood film; one often sees nuclei with only a few granules adherent, the majority having become detached from the cell. In fact one almost receives the impression that the cell itself actively discharges its granules, in a more or less explosive manner. In the neutrophile leucocytes the granules, as in the dogfish, are distinctly rod-shaped. The erythrocyte is formed from the small round cell as in the dogfish, but its nucleus undergoes very little shrinkage or condensation during the process of its development, and so the nucleus of even the adult red blood cell is almost identical with that of the parent small round cell. One can also see all the stages intermediate between the small round cell and the fully developed granulocyte. Giant erythrocytes occur, and possess many points of resemblance to the megaloblasts of human blood. They are about twice the size of the ordinary erythrocyte, but have a relatively much larger nucleus which is markedly reticular, while their cytoplasm is poor in haemoglobin. They are not red cells about to divide, as no intermediate forms occur of direct or indirect division. They appear at first sight to be erythrocytes which are developing from large instead of from small round cells. Even this is doubtful, however, and probably they are normal intermediate forms in erythrocyte formation, for reasons shortly to be mentioned.

BLOOD FORMATION

A full account of the literature concerning the morphology and development of the blood in Fishes is given by Dean (13). Giglio-Tos (21) in 1896 described blood formation in the lamprey, and showed that it was localised in the spiral valve of the intestine. Bryce (7, 8) in 1905 gave an interesting account of haemopoiesis in the larva of *Lepidosiren paradoxa*; the conclusions arrived at in this paper agree almost exactly with his. Weidenreich (87) in 1905 gave an excellent critical summary of all the previous work. Rawitz (74) in 1899 and Werzberg (88) in 1911 also made extensive investigations into the morphology of Fishes' blood. Werzberg's paper in particular is very valuable, as he examined a large number of Fishes.

It is clear from the accounts already given that as far as Elasmobranchs are concerned (and the same applies to Teleosts also) the evidence is definitely against the polyphyletic theory of blood formation, and in favour of the

monophyletic theory. In the Elasmobranchs this fact stands out with extraordinary clearness. The common ancestor of the various blood cells would appear to be a small round cell, consisting mainly of nucleus, with little or no cytoplasm. It is by reason of the initial scantiness of the cytoplasm that differentiation into such widely divergent cell types as the erythrocyte and the granulocyte becomes possible, such differentiation depending primarily upon the kind of cytoplasm which this small round cell acquires, and secondarily upon changes in the nucleus following the acquisition of this cytoplasm. The scheme given by Bryce (8) to illustrate the second or post-larval phase of haemopoiesis in *Lepidosiren paradoxa* applies almost equally well to blood formation in the adult Elasmobranch:



The first step in the evolution of the small round cell into the erythrocyte is a slight swelling of the nucleus and the acquisition of a narrow rim of cyto plasm, which at first contains little or no haemoglobin. This cytoplasmic rim is usually homogeneous in its early stages; as it grows the haemoglobin content progressively increases. At the same time small rod-shaped actively motile bodies make their appearance in the cytoplasm. In a blood film prepared in the ordinary manner they do not stain, but they stand out very clearly when stained by a "vital" stain such as brilliant cresyl blue or neutral red. They do not stain with janus green B. They are not present in the very young red cell; they disappear almost completely in the adult red cell. In the intermediate stages they are very numerous and conspicuous. Giglio-Tos described similar "granulations" in the lamprey, and Sabrazes and Muratet (78, 79) in some other fishes. Giglio-Tos's view that they represent haemoglobin-forming substances is highly probable, for by the time the erythrocyte has acquired its full complement of haemoglobin they have disappeared. The acquisition of haemoglobin only proceeds up to a certain stage, at which the erythrocyte is said to be mature. At the same time as the cytoplasm is increasing the nucleus also enlarges, and becomes reticular, but with further increase in the cytoplasm the nucleus undergoes retrogressive changes, becoming shrunken and condensed.

What exactly are the limiting factors which allow the growth of the cell to proceed so far and no further it is difficult to say. The blood cells are different from the cells of most other tissues in that once they enter the blood stream they cease to be under the control of the central nervous system;

and they are also free from another growth-limiting factor, the pressure of adjacent cells. Therefore one must assume one of two things. Either there is some chemical agent present in the circulating blood which prevents the further growth of the cells once they have entered it. For this some of the recent work on tissue culture seems to hold some justification (3, 9, 10, 11). Or else the check may come not from without, but from within the cell itself; the specialisation of the cytoplasm has a nocuous effect upon the nucleus, and so upon the cell as a whole, so that it undergoes a degenerative process sufficient to prevent it from multiplying, but not to cause its complete breakdown. The fact that the nucleus of the mature cell is atrophic would fit in equally well with either hypothesis, the only question being one of *post hoc* or *propter hoc*.

The development of the erythrocyte from a non-haemoglobiniferous small round cell has been described by numerous observers (29, 42, 56, 88). Bizzozero (5) maintains that every erythrocyte is only formed by the division of a pre-existing erythrocyte, while Jolly (30), agreeing with Bizzozero that this mode of erythropoiesis occurs, at the same time does not exclude its formation from the small round cell. As far as the present work is concerned all one can say is that the erythrocyte in the vast majority of cases develops directly from the small round cell. The mature erythrocyte is quite definitely incapable of division, for when pyknosis occurs further nuclear activity is out of the question. It is, on the other hand, more than probable that the immature erythrocyte is capable of division. It is often very difficult to decide whether these dividing cells contain haemoglobin or not; if they do it can only be in small quantity, and not in the amount present in the mature cell.

Bizzozero's great objection to the development of the erythrocyte from the small round cell is that he does not believe a non-haemoglobiniferous cell can ever acquire haemoglobin. The obvious answer is that the first erythrocytes which come into existence certainly acquire their haemoglobin somehow, so that the development of haemoglobin in a cell which did not previously contain it, far from being impossible, does actually occur at one stage of development; and there is no reason why it should not occur again. Jolly, while believing that the erythrocyte can divide to form fresh red cells, asserts that before it does so it first of all loses its haemoglobin, and the daughter cells formed by its division have to reacquire their haemoglobin *de novo*. Thus, while agreeing with Bizzozero in the power of the red cells to divide, he disagrees with Bizzozero's main objection to the other method of erythropoiesis, namely from a non-haemoglobiniferous cell. Jolly's main work, it may further be noted, was carried out on amphibian blood, not fishes', and it is possible that there may be considerable difference between the two.

The first step in the development of the granulocyte from the small round cell resembles very closely the first step in the formation of the erythrocyte, and consists in the acquisition of a narrow rim of granular cytoplasm; the granules at first are not as large, nor do they stain so deeply, as those of the

adult cell. In the early stages of their growth the nuclei of the erythrocyte and the granulocyte are exactly the same. As a result of nuclear changes however the two cell groups diverge still further from the parent type. In the case of the erythrocyte the nuclear change is one of shrinkage and condensation. In the case of the granulocyte there is only slight condensation, but together with it there occurs lobulation, so that the nucleus may ultimately form two or even three distinct lobes, as in the adult perinucleate cell. Drzewina (15) had some idea of this possible development of the granular cell from the lymphocyte, observing in the lymphoid tissue of the sturgeon's kidney a whole series of intermediate forms between the two types of cell, but she did not come to any definite conclusion. In the present work these various transition stages have been met with so frequently, in all the Elasmobranch spleens examined, that there is no room for doubt in the matter. Lowitt (42) believed that there were two different types of small round cell, from one of which the erythrocyte developed, from the other the granulocyte. In the Elasmobranch spleens, more particularly in those of the ray and skate, there seems at first sight to be some evidence of this being so. But careful examination shows that what actually happens is that the nucleus of the small round cell begins to undergo slight changes very early on, before it has acquired any obvious coating of granules or haemoglobin.

The method used in the present work for the production of anaemia has already been described. Jolly (30), using *Triton cristatus*, produced anaemia by starving the animal for three to five months and then feeding abundantly with "red worms." This procedure results in widespread mitosis of all the body cells, including the red blood corpuscles. One can hardly doubt the accuracy of Jolly's findings, but at the same time it seems clear that prolonged starvation induces a totally abnormal state of affairs, and one must exercise great caution in making deductions therefrom as to the normal method of blood formation. Starvation for example would create a shortage of haemoglobin, in virtue of which it seems more than likely that none of the erythrocytes would ever become fully mature, and in consequence the final nuclear changes of shrinkage and condensation would not supervene. It is therefore highly probable that the dividing erythrocytes observed by Jolly were all immature forms. Clearly the immature erythrocyte is much more likely to be capable of division than the mature erythrocyte. For the small round cell can undoubtedly multiply, and the young erythrocyte, before degenerative changes have occurred in its nucleus, is after all only a small round cell with a little cytoplasm added.

Laguesse (36), working with trout embryos, produced anaemia by cutting off their tails. Bizzozero and Torre (5), working with *Carassius auratus*, bled the animals four times in fourteen days by cutting on each occasion one of the branchial arteries. In both these instances it is very difficult to gauge the degree of anaemia produced. In the present work, on the other hand, the degree of anaemia could be estimated with considerable accuracy, and as

may be seen from the appended list, 37 per cent. of the total blood was withdrawn on the average, and in some cases 50 per cent. or over.

In Bizzozero's experiments fresh blood formation (in the form of mitosis of erythrocytes) was not observed until sixteen days after the last bleeding, or thirty days after the first. In the present work the animals were examined at intervals varying from six to thirty-one days after the withdrawal of blood. New blood formation begins to be evident by about the sixth day, reaching a maximum about the twentieth, as indicated by the appearance in increased numbers of immature cells both in the blood and the spleen. The only undoubted method of blood formation observed was that which has already been described, namely from the small round cell. No mitoses of granulocytes were observed throughout the entire series; occasionally mitoses were seen which might have been either small round cells or immature erythrocytes.

THE SPLEEN IN THE TELEOSTS

Of the Teleosts the following members have been examined: *Pleuronectes platessa* (plaice), *P. flesus* (flounder), *P. limanda* (lemon-dab), *P. microcephalus* (common dab), *Gadus merlangus* (whiting), *G. minutus* (poor cod), *G. luscus* (whiting pout), *G. pollachius* (pollack), *G. morrhuae* (common cod), *Lophius piscatorius* (angler-fish), *Trigla gurnardus* (grey gurnard), *Morone labrax* (salmon bass), *Molva molva* (ling), *Spinachia vulgaris* (fifteen-spined stickleback), *Callionymus lyra* (dragonet).

Generally speaking, the Teleosts are a much larger and more heterogeneous group than the Elasmobranchs. The three main splenic elements, lymphoid tissue pulp and ellipsoids, are present in all except the dace, where the ellipsoids seem to be almost completely absent.

The capsule is like that of Elasmobranch spleens, except that in many Teleosts there are often to be found embedded in it varying amounts of pancreatic tissue. These outlying fragments of pancreas sometimes follow the track of the splenic vessels into the interior of the spleen. This is well marked in the *Pleuronectes* and *Gadus* families, and best of all in *Molva molva*. The pancreatic elements are always separated off from the splenic substance proper by a layer of fibrous tissue. As in Elasmobranchs so in the Teleosts there is no trace whatever of muscle in the capsule, or of a trabecular system. In *Trigla gurnardus* there are a few delicate septa of fibrous tissue passing from the capsule for a very short distance into the splenic substance.

The ellipsoids show some interesting variations in different species. In *Lophius piscatorius* the reticular meshwork in the ellipsoidal wall stands out very clearly, while surrounding the ellipsoids are large sinus-like spaces. These spaces only occasionally contain blood, and then in small quantities; it would appear that they are occupied mainly by lymph. They have a definite endothelial lining and are traversed by fine strands of connective tissue passing between the ellipsoid and the outer wall of the sinus. Most Teleosts show very

clearly the presence of disintegrating erythrocytes in the ellipsoidal walls. The ellipsoids attain a particularly high degree of development in *Molva molva*. Here they are often eccentric in shape, and have numerous gaps in their walls. In a Mallory stained section it may be seen that the condensed sheet of connective tissue which surrounds the ellipsoid becomes thinned out and deficient opposite these gaps, through which blood seems to pass to enter the pulp, and the main axial lumen of the ellipsoid often seems to end blindly. Pouchet (72) has described this method of ellipsoidal termination as occurring in Elasmobranchs, but this I have been unable to confirm.

Lymphoid tissue tends to be more diffuse in Teleosts than in the Elasmobranchs. It is very well developed in *Molva molva*, and tends to form definite nodules in *Morone labrax*. In most Teleosts however lymphoid tissue seems very diffuse, sometimes almost inextricably intermingled with the pulp. One very distinctive feature is the development in Teleostean lymphoid tissue of pigment nodules. These were present in all the spleens examined, with the exception of *Spinachia vulgaris*. In addition to their association with lymphoid tissue, the pigment nodes sometimes (e.g. in the flatfishes) have definite vascular relationships, surrounding the smaller arteries and veins. They also occur in the lymphoid deposits found in other parts of the body besides the spleen, e.g. the lymphoid tissue of the kidney (fig. 3). They have a fairly sharply circumscribed outline as a rule, though there is usually no definite connective tissue layer surrounding them to account for this appearance. As a rule they are paler towards the centre, and darker towards the periphery. Their chief contents are small spherical masses of brown or greenish brown pigment, which may often be observed to consist of small closely packed brownish granules. Occasionally one receives the impression that these masses are pigment-containing cells, as there may be a suspicion of a nucleus present; usually however this is not the case. In addition there are frequently, though not always, to be found in the pigment nodules erythrocytes and small round cells in the process of disintegration. The pigment nodes are rich in lipoids in their central clear portion. Histo-chemical tests for iron also show that they have a high iron content. The pigment is quite evident even in unstained sections, but curiously enough one sees very little of it in splenic smears. The colour of the pigment is strongly suggestive of bile, a view which is favoured by the frequent occurrence of disintegrating red cells. Similar pigment masses, more numerous but smaller in size, are to be found in the dogfish's liver.

The details of haemopoiesis were much more difficult to follow in Teleosts than in Elasmobranchs. In those cases where it was possible to come to any conclusion, the usual mode of erythropoiesis was seen to occur. The gurnard (*Trigla gurnardus*) shows two interesting phenomena in connection with the development of the red corpuscles. The parent small round cell has in its cytoplasm large basophile granules. As the cell enlarges and acquires its coating of haemoglobin, these granules become smaller and fewer. Just before

the final stages of erythrocyte formation, the cell cytoplasm consists of small scattered bluish granules on a dull pink background. The appearance resembles very strikingly the condition of punctate basophilia found in human blood in Addisonian anaemia, although of course it is not suggested that there is any analogy between the two, or that the occurrence of punctate basophilia in human beings indicates a reversion to a piscine ancestry.

In the *Gadus* group the erythrocytes may assume a very curious shape. At first round, they then become oval, as in other fishes. They then show an increasing tendency towards angularity, and finally may become perfectly triangular in shape (fig. 15). The relative proportion of triangular to oval red blood corpuscles varies from one animal to another. The illustration shown is from a blood film of *Gadus minutus* in which the majority of the erythrocytes are triangular. On the other hand there are many cases in which only a few of the corpuscles are triangular, and the majority are of the normal shape. The triangularity is not artificially produced by the fixative because it may be observed in specimens of perfectly fresh and unfixed blood, though the angles may not be sharp as in the fixed film.

Another interesting variation which may occur is connected with the nucleus of the erythrocyte. It has already been observed that in the course of development of the small round cell into the erythrocyte or the granulocyte, there is in each case a certain amount of nuclear degeneration, such degeneration in the case of the erythrocyte taking the form of shrinkage and condensation, whereas in the case of the granulocyte the nucleus becomes lobulated. In the erythrocytes of the *Pleuronectes* group quite frequently, and in other Teleosts occasionally, the nuclei of the erythrocytes also may be lobulated.

The granulocytes in Teleosts are not very well marked. Eosinophiles in particular are sometimes very inconspicuous, so much so that Sabrasez and Muratet (quoted from Bashford Dean's bibliography) believed them to be absent altogether from Teleost blood. This however is not the case. In the *Gadus* family they are quite numerous and easily found. But it is certainly true that they are not as uniformly plentiful or as intensely eosinophilic as they are in Elasmobranchs. In *Trigla gurnardus* the neutrophile leucocyte possesses both basophile and eosinophile granules, the basophile surrounding the nucleus, and the eosinophiles occupying the periphery of the cell. The cell would more correctly be called ambophile. A similar phenomenon has been noted by Drzewina in other fishes, and she questions the orthodox view as to the specificity of the granulocytes, at any rate as far as lower Vertebrates are concerned. It is quite common in most Fishes to note that the pinkish granules of the neutrophiles lie against a faint blue background, but the blue-staining substance is not granular.

In the blood of the gurnard (*Trigla gurnardus*) there occur giant erythrocytes, and their occurrence raises the very important question "What is the mechanism which ensures that the growth of the erythrocytes shall only

proceed up to a certain point?" With this is associated the question as to why all the erythrocytes should be of the same size. In addition to what has been observed previously, in considering why cells circulating freely in a fluid medium should cease to grow at all, there is an important mechanical factor to be taken into consideration, and that is the bore of the capillary through which the erythrocytes have to pass. If the diameter of the erythrocyte is greater than that of the capillaries, it will undergo compression each time it passes through, causing after frequent repetition its elongation in the line of the long axis of the capillary, and its shortening in the direction of its compression, that is transversely to the line of blood flow. In this way, by compression in one axis and elongation in the other, one may possibly have an explanation for the change in shape of the erythrocyte, from the spherical when it is young and attached to the lymphoid tissue, to the oval as it matures and enters the general circulation, where it is subjected to the moulding action of the capillaries. One might of course argue in the opposite direction, that the bore of the capillaries is determined by the size of the erythrocytes which force their way through. But that could only apply very early on in development when the capillaries are first being formed. Once the capillaries are fully formed and their mean calibre fixed, one would suppose that the blood cells have little, if any, further action upon them, whereas their influence upon the blood cells will continue throughout life, as long as blood is being formed. If for any reason (such as the parent cell being larger than usual or possessed of greater developmental activity) the erythrocyte grows more than the normal, it can easily grow to twice its length and still be able to traverse the capillaries, but it cannot grow in width with quite the same facility. Hence one would expect giant erythrocytes to be only a little wider than normal, but considerably longer; and this is what actually happens. In the blood of the gurnard the average erythrocyte measures $6\mu \times 8\mu$, and the giant variety $7{\cdot}5\mu \times 14\mu$.

The nuclear degeneration in the erythrocyte of Fishes does not usually proceed beyond the stage of shrinkage and condensation. In exceptional cases however this state may be followed by one of chromatolysis, the nuclear substance then mixing with the remaining part of the cell to a greater or lesser degree. In Mammals of course this mixture of nuclear substance is normally complete, giving rise to the homogeneous mass which constitutes the mammalian red blood corpuscle. It is important however to note that this is not an absolutely new phase in the life cycle of the erythrocyte, developing exclusively in Mammals, but on the contrary that indications of it may be seen in the blood of even such primitive Vertebrates as Fishes.

SUMMARY AND CONCLUSIONS

1. The present paper is based upon a detailed examination of the spleen, blood, and kidneys of a number of Fishes.

2. The Fishes examined are *Calamoichthys, Scylliorhinus canicula, Scylliorhinus catulus, Raia clavata* and *Raia batis, Pleuronectes platessa, P. flesus, P. limanda* and *P. microcephalus, Gadus merlangus, G. morrhua, G. luscus, G. pollachius* and *G. minutus, Lophius piscatorius, Trigla gurnardus, Morone labrax, Molva molva, Spinachia vulgaris, Callionymus lyra,* and *Leuciscus leuciscus.*

3. A modification is described of the ordinary technique for making smear preparations of the spleen or any other cellular tissue. There is also described a method for the application of Leishman's stain to paraffin sections.

4. In the Dipnoi (Lung Fishes) there exists a very primitive type of splenic circulation, arranged so that the blood may flow around the lymphoid tissue and receive from it the developing blood cells.

5. In the Elasmobranchs (Cartilaginous Fishes) there is to be observed an essentially similar arrangement, the splenic circulation being so designed as to enable the blood to circulate through the pulp and around the lymphoid tissue.

6. The same may be said of the Teleosts, but on the whole the arrangement of the splenic elements is much less precise in the Teleosts than in either the Dipnoi or the Elasmobranchs.

7. In Elasmobranchs, most markedly in the dogfish, the ellipsoids contain in their walls lipoid granules; in paraffin sections where these granules do not show, there is to be seen in the wall of the ellipsoid a fine reticular formation.

8. In most Fishes (e.g. the ray, plaice and ling) there are present in the wall of the ellipsoid red blood corpuscles in various stages of disintegration. It is inferred from this that the ellipsoids play an important part in the mechanism of blood destruction. The ellipsoids also help in the removal of foreign particles from the blood stream.

9. The capsule in all the fishes examined is very thin, and consists of a single layer of epithelium with a thin stratum of fibrous tissue underneath. Muscular tissue is not present, and there are only a few elastic fibres. There is no indication whatever of a trabecular system.

10. The pulp consists of a spongy cellular reticulum through which the blood percolates.

11. In all the Elasmobranchs examined, and in the vast majority of the Teleosts, the arteries terminate by dividing into three or four short thick-walled capillaries, the ellipsoids, which open directly in the spaces of the pulp reticulum. The veins commence by the confluence of these pulp spaces, so that the circulation through the spleen is unquestionably open. There are no ellipsoids in the Dipnoi, if one may generalise from the single specimen examined, but there also the circulation seems to be an open one.

12. The region where pulp and lymphoid tissue adjoin one another has been called the boundary zone; in the boundary zone there is no connective tissue barrier between the pulp and the lymphoid tissue, and cellular interchanges occur in this region quite freely between the lymphoid tissue and the pulp.

13. The lymphoid tissue of Fishes gives rise to all the cellular elements of the blood. In Teleosts it is also the seat of certain pigmentary changes whose precise significance is obscure. Although the term "lymphoid" is retained in this paper, the tissue so named is very different from the lymphoid tissue of Mammals.

14. The lymphoid tissue of Fishes is composed mainly of aggregations of small round cells. These cells have a relatively large spherical nucleus, with little or no cytoplasm.

15. The original small round cells may develop into either erythrocytes or granulocytes. This process may be best seen in the Elasmobranchs.

16. In order to demonstrate the phenomena of haemopoiesis more clearly, blood formation was stimulated in a number of dogfishes by the experimental production of anaemia. Full details of the technique and the results obtained are given in the text.

17. The blood cells in Elasmobranchs, and in all those Teleosts where it was possible to form a definite opinion, are derived from one common parent cell.

18. The occurrence of abnormally large erythrocytes leads to a consideration of the factors which control the growth of the blood cells. No satisfactory conclusions are reached.

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DESCRIPTION OF FIGURES AND ILLUSTRATIONS

Fig. 1. Smear of dogfish's spleen (× 60) prepared in the ordinary manner. Note the confused arrangement of the cells and the artificial cell processes.

Fig. 2. Smear of dogfish's spleen, made according to the technique described for the anatomical smear. Note the absence of cell processes. *S* = the lighter coloured area in the middle of the field corresponding to the lumen of a blood vessel. It is surrounded by more closely packed small round cells.

Fig. 3. Kidney of *Pleuronectes platessa* (plaice) (× 60). *T* = renal tubules cut in transverse section. *L* = an irregular mass of lymphoid tissue in between two tubules. *P* = a pigment node, showing in the photograph as a black area in the midst of the greyish lymphoid tissue. There are no glomeruli to be seen in the section; they seem to be much more infrequent in the kidney of Fishes than in higher Vertebrates.

Fig. 4. Spleen of *Calamoichthys* (× 60). *A* = the thick-walled splenic artery, with blood in its lumen. *V* = the thin-walled splenic vein, whose lumen is empty. *v* = a tributary of the splenic vein, arising in the pulp and coursing through the sheath of lymphoid tissue in which the main artery and vein are situated, somewhat eccentrically.

Fig. 4 *a*. Schema, based upon fig. 4, to illustrate the essentials of the splenic circulation in *Calamoichthys*. The central artery and vein are surrounded by lymphoid tissue, and outside this is the pulp, which, for the sake of clearness, has not been drawn in. Blood flows from the artery (*A*) through the lymphoid tissue, and then through the pulp, in the direction of the arrows, *around* the lymphoid tissue, and then back through the lymphoid tissue again to the vein (*V*). The cells in that portion of the lymphoid tissue which immediately adjoins the pulp are beginning to differentiate. *Er'* = a lymphoid cell which is just beginning to acquire a coating of haemoglobin-containing cytoplasm and to develop into an erythrocyte. *Er''* is a similar cell in a more advanced stage of development. *Er* = a mature erythrocyte in the pulp.

Fig. 5. Spleen of dogfish (*Scylliorhinus canicula*) stained with Leishman. *E* = an ellipsoid in transverse section. There are several other ellipsoids cut more obliquely. Note the blood in the lumina. *LV* = a blood vessel surrounded by lymphoid tissue. The lymphoid tissue is stained blue, the pulp red.

Fig. 6. Spleen of dogfish (× 250) washed out with normal saline and then perfused with Zenker-formol. *S*, *S*, *S* = pulp spaces in between the cells of the pulp reticulum and their processes. *V* = small vein formed by the coalescence of several pulp spaces. *E* = an ellipsoid.

Fig. 7. Spleen of dogfish (× 250) prepared by perfusion-fixation. *W* = wall of ellipsoid. *L* = lumen of ellipsoid. Two arrows have been drawn in the lumen of the ellipsoid, which is dividing into two and entering the pulp spaces. Compare with fig. 6. Figs. 6 and 7 together show that the circulation through the pulp of the dogfish's spleen is unquestionably an open one.

Fig. 8. Spleen of dogfish (× 250), showing junction between an arteriole (in a lymphoid sheath) and an ellipsoid. *WE* = wall of ellipsoid. *LE* = lumen of ellipsoid. *LL* = lumen of lymphoid vessel.

Fig. 9. Drawing of ellipsoid from dogfish's spleen; transverse section. *L* = lumen of ellipsoid. *P* = process from wall of ellipsoid to join with a cell of the pulp reticulum. *R* = reticulum cell of pulp. *Er* = erythrocyte lying in a space of the pulp reticulum. *Gr* = small pigment granules in wall of ellipsoid.

Fig. 10. Spleen of dogfish (× 500). High power view of lymphoid tissue. *H* = large hyaline cells, scattered among the smaller lymphoid cells. Note the cytoplasm of the hyaline cell, which is practically unstained.

Fig. 11. Cells from a smear preparation of dogfish's spleen (× 1500). Nos. 1–7 represent various stages in the development of the small round cell into the erythrocyte. Nos. 8–13 represent stages in the course of its development into the granulocyte. (Stained with Leishman's stain.)

Fig. 12. Section of dogfish's spleen, passing through the boundary zone. It will be seen that there is no sharp demarcation of the pulp, lying in the lower and right-hand portion of the drawing, from the lymphoid tissue lying above and to the left. The pulp is stained predominantly red, the lymphoid tissue blue. *Er* = two stages in the development of the small round cell into the erythrocyte. *Gr* = stages in the development of the small round cell into the granulocyte. The actual details of these changes are much better seen in smear preparations. The section is necessary however to show the micro-anatomical position of the cells.

Fig. 13. Spleen of dogfish. Frozen section stained with Sudan III (× 250). The yellow staining lipoid granules show up black in the photograph. *LG* = lipoid granules.

Fig. 14. Spleen of ray (× 250). In the middle of the field is an ellipsoid cut in transverse section. There is blood (showing black in the photograph) in the lumen. *Er* = an erythrocyte in the wall of the ellipsoid. Although it is not obvious in the photograph, in the actual slide the erythrocyte is quite obviously undergoing disintegration.

Fig. 15. Blood of *Gadus minutus* (× 625) showing triangular red blood corpuscles.

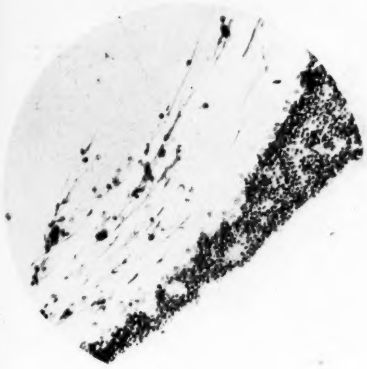
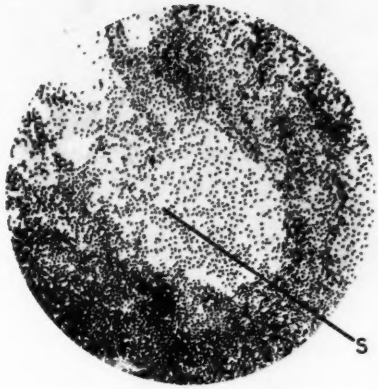


Fig. 1.



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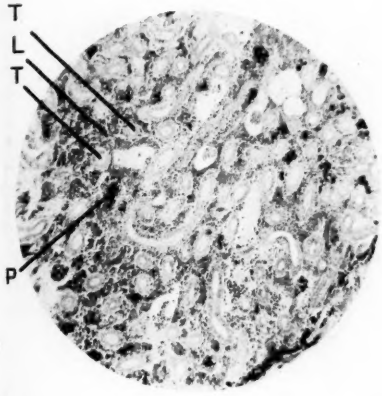


Fig. 3.

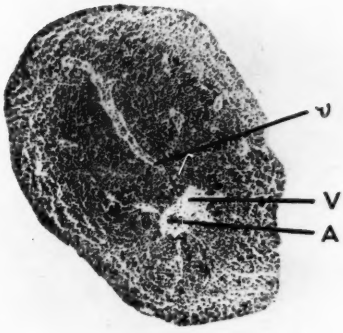


Fig. 4.

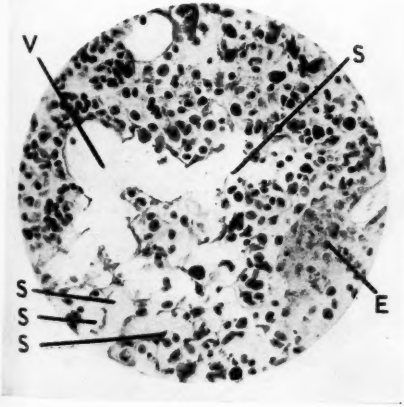
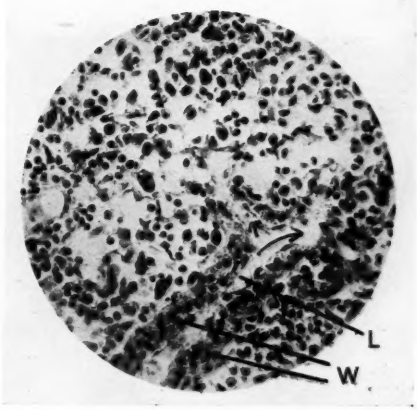


Fig. 6.



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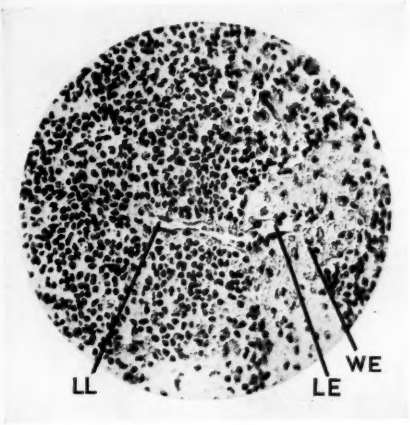

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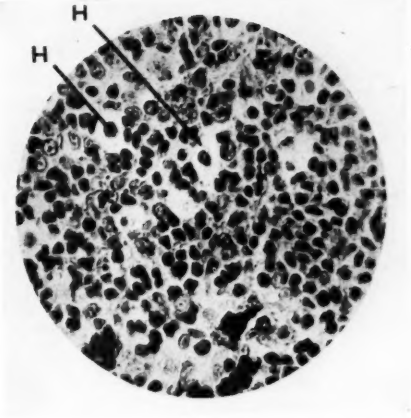

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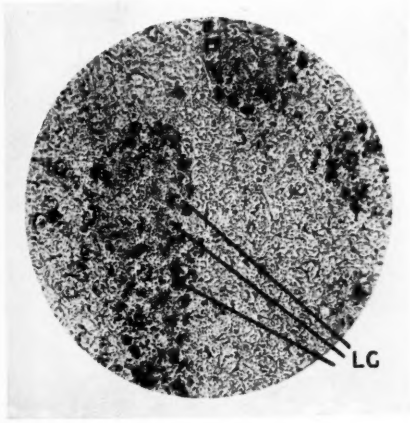
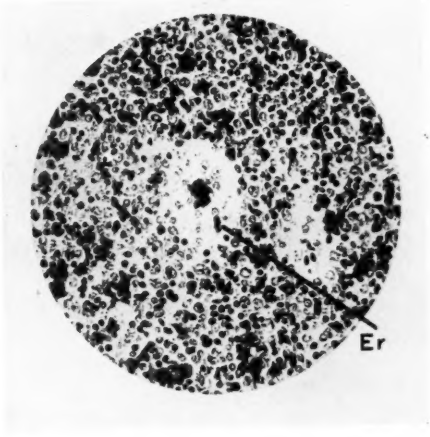


Fig. 13.



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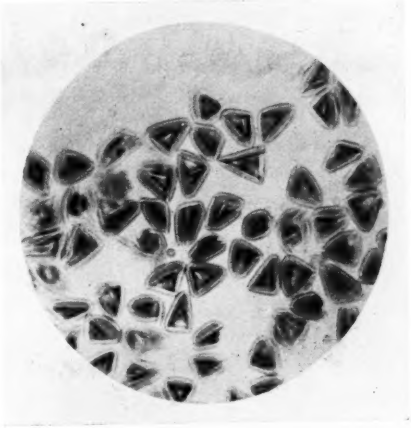


Fig. 15.

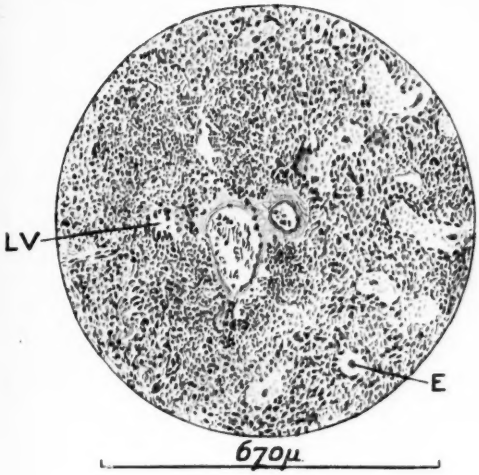
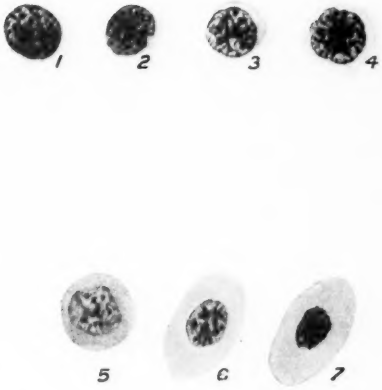


Fig. 5



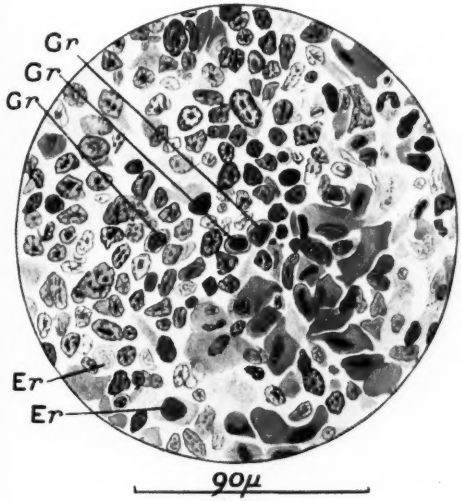


Fig. 12

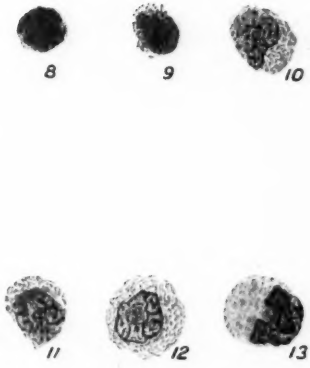


Fig. 11

THE TECHNIQUE OF ESTIMATING SMALL IRREGULAR AREAS IN BIOLOGICAL RESEARCH, WITH NOTES ON THE TESTS OF ACCURACY

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INTRODUCTION

In biological investigations there is an increasing tendency to establish numerical relationships between phenomena. While following this tendency the morphologist meets with considerable difficulties which arise from the complexity of the objects that he studies, and which materially reduce the accuracy of the results obtained. Investigations which entail difficulties of this kind are those in which surfaces of irregular outline are to be measured with a view to estimating, for example, the relative amounts of different tissues in sections of an organ, or the ratio of nuclear volume to cytoplasmic volume in a cell, or, again, the rates of growth of various organs. In a valuable contribution to this technique, Scammon and Scott (1927) have analysed some of the sources of error inherent in different methods. They have shown, in the first place, that a 7-inch Amsler polar planimeter is by no means sufficiently accurate, especially for small areas (circles of about 1 cm. in diameter).

A second method commonly used for the determination of irregular areas is the area-weight method, whereby pieces of paper of the required shapes and sizes are cut out and weighed, and, if the paper is of uniform thickness, values proportional to the areas are obtained. This method Scammon and Scott (1927) consider to be more accurate than the planimeter method, but still liable to error. Finally, these authors have discovered that sheets of celluloid composition are less liable to introduce errors than is paper.

Probably owing to its tediousness, the use of squared paper in such estimations is not by any means common. It is, however, sometimes necessary to ascertain very accurately the relative sizes of small irregular areas, such as the images of chromatin particles, of small groups of cells, or of bacteria, in a microphotograph or *camera lucida* drawing, or, perhaps, the cerebral convolutions of very small animals; and in such cases the question arises whether the accuracy of the squared-paper method would compensate for its tediousness.

In the course of researches now being conducted upon the early development of Mammals, it was desired to examine in this way drawings of chromatin particles, the areas being about 4 or 5 sq. mm. The two planimeters examined (Amsler's No. 3, and Ott's compensating polar planimeter) were obviously not of sufficiently fine calibration for such areas. It was therefore decided to

compare as regards accuracy the squared-paper method with that in which celluloid is used, with particular attention to areas smaller than those treated in Scammon's and Scott's investigations. Moreover, these investigators purposely confined attention to the variability due to the material (paper or celluloid). Thus, their paper and celluloid discs were not traced by hand and then cut, as would usually be done in investigations of organs or tissues, but were punched out by hollow steel cylinders. Upon the results of Scammon's and Scott's minute and carefully controlled observations are based the present tests; but in these the conditions have resembled to a fair extent those under which the methods would be actually practised.

METHOD OF TESTING ACCURACY

To determine the relative accuracy of different techniques in such a case, elementary statistical methods must be employed. Wherever cells or tissues are compared numerically, tests should be carried out, in order that it may be fully appreciated how far the results are really significant, and it is regrettable that even within recent years records have appeared which show no evidence that tests of error have been performed. Since such tests frequently involve the elementary statistical treatment employed in the present investigation, it will perhaps be of use to record this treatment in some detail.

In some instances, as will be shown, the observations were made by weighing, in others by measurement of areas; but in either case twenty-five observations were made, and from them the arithmetic average or mean was calculated. The object was to ascertain how far the readings were liable to deviate or vary from the average—a variation due to a number of causes, such as lack of uniformity in the material (squared paper and celluloid) and imperfections in manipulation (tracing and cutting). For this purpose the average deviation might be calculated, i.e. a simple average of the differences between the various readings and the mean, all the deviations being considered of positive sign. Instead of this, however, the "standard deviation" is commonly used, especially in biology. Although more difficult to calculate, it has the advantage of laying rather more stress on the larger deviations than does the average deviation. The standard deviation is obtained (Elderton, 1927, pp. 50–1) by finding the differences between the various observations and the average; squaring these differences; adding them together; dividing by the number of observations, and extracting the square root of the result[1]. Roughly, three times the standard deviation on either side of the arithmetic average

[1] An apparently more cumbrous, but actually a simpler method is the following, quoted from King (1921, p. 149): "Select some whole number approximating to the arithmetic average; compute the deviations therefrom; square each; summate; subtract therefrom n times the square of the difference between this number and the true average; divide by n; extract the square root of the quotient." (n is the number of observations, here 25.)

It may be remarked that even those of us whose interests or daily pursuits are non-mathematical find this and other of the simpler statistical methods soon repay the labour involved.

will include all the variates or various observations of which the sample (here 25) has been taken (Pearl, 1923, p. 274).

Certain of the results, however, are expressed in milligrammes and others in square millimetres, and it is impossible immediately to state whether there is greater liability to deviation in the one set or in the other. For this purpose the "coefficient of variation" is employed, which is the standard deviation expressed as a percentage of the average of the series (Pearl, 1923, p. 275).

The mean itself is liable to error. This liability will be small in cases where there are many observations closely equivalent to the mean, i.e. when the standard deviation is small (Elderton, 1927, p. 76), and therefore its liability to deviation can be expressed partly in terms of the standard deviation of the series. The accuracy of the mean naturally also depends on the number of observations. It has been found that this relation is not direct but that the accuracy depends on the square root of the number of observations. Taking four times the number of observations merely doubles the accuracy. Hence the deviation to which the mean is liable is obtained by dividing the standard deviation by the square root of the number of observations. Usually 0·6745 times this number is employed, and is called the "probable error" of the mean. The probable error is of value because, when the difference between two means exceeds three times its own probable error, it is considered significant (Elderton, 1927, p. 79; cf. Pearl, 1923, p. 214). (It may be pointed out that the standard deviation itself is of equal value as a test of significance. The use of the probable error is largely a matter of custom.)

In Test I (*a*) below, the standard deviation of the series of twenty-five readings is ± 0·311. Therefore the deviation to which the mean is liable is $\pm \frac{0{\cdot}311}{\sqrt{25}} = \pm 0{\cdot}062$. The probable error of the mean is therefore

$$0{\cdot}6745 \times (\pm\, 0{\cdot}062) = \pm\, 0{\cdot}042,$$

and the average is expressed as 4·144 ± 0·042.

The probable errors of the standard deviation and of the coefficient of variation have also been calculated (*v.* Pearl, 1923, pp. 274–5), and are inserted at the appropriate places below.

MATERIALS

In the subsequent tests the materials used were:

Thin paper ruled in square millimetres.

A hard pencil for the drawing of the outlines on the squared paper.

Sheets of "Eastman Kodaloid No. 3," the celluloid preparation employed by Scammon and Scott (1927). This material is used in the making of photographic films, and No. 3 has a thickness of approximately 0·135 mm.

Sharp pointed styles, for marking the kodaloid.

A swivel knife. This type of knife, employed by show-card writers in cutting out curved figures, is manufactured by the Paasche Airbrush Co. of Chicago;

it can be more accurately manipulated than scissors, and is to be recommended especially where irregular figures have to be cut.

An analytical balance sensitive to one-fifth of a milligramme.

A fine pair of draughtsman's compasses, capable of being set by a screw.

A hollow steel cylinder or punch.

TESTS AND RESULTS

The tests performed were as follows:

I (*a*). Twenty-five circles were drawn on the squared paper by means of the compasses. The areas were then estimated by counting the squares and fractions. (In this and the subsequent tests, only the parts completely within the boundary lines of the areas were counted.)

Average area (sq. mm.) = 4·144 ± 0·042.
Standard deviation (sq. mm.) = ± 0·311 ± 0·030.
Coefficient of variation (per cent.) = 7·51 ± 0·720.

I (*b*). A tracing on kodaloid of each of the circles of I (*a*) was made by means of a style. The discs were cut out with the swivel knife and weighed.

Average weight (mgm.) = 0·952 ± 0·054.
Standard deviation (mgm.) = ± 0·398 ± 0·038.
Coefficient of variation (per cent.) = 41·78 ± 4·63.

The coefficient of variation in I (*b*) is very great. (Compare also the results of Test III (*a*) below.) Under the circumstances described, therefore, the conclusion is that the use of squared paper leads to much less variable results (7·5 per cent. variability) than those obtained by the use of kodaloid (42 per cent. variability). The squared-paper method was actually found to be the quicker and less laborious method for such small areas.

II (*a*). As it was thought possible that the compasses used in Test I had introduced an error affecting both I (*a*) and I (*b*), small round areas were marked on the squared paper by pressing it against a block of cork by the sharp end of a metal cylinder or punch. Twenty-five observations were made.

Average area (sq. mm.) = 5·87 ± 0·057.
Standard deviation (sq. mm.) = ± 0·425 ± 0·041.
Coefficient of variation (per cent.) = 7·24 ± 0·694.

There is therefore no significant difference between this result and that of I (*a*), and thus the use of compasses was a sufficiently satisfactory means of making test circles.

II (*b*). The same style, made slightly sharper, was used to punch out twenty-five kodaloid discs, each of which was then weighed.

Average weight (mgm.) = 1·584 ± 0·0073.
Standard deviation (mgm.) = ± 0·054 ± 0·0052.
Coefficient of variation (per cent.) = 3·43 ± 0·327.

The variation in this series is under half that of the corresponding series of actual areas (II (*a*)). It will be noted that a difference of 0·1 mgm., which

the balance used is not designed to detect, would correspond to a difference in area of about 0·35 mm., which would certainly be detected. Relative insensitiveness of the balance may therefore produce a fictitious uniformity of results.

It will further be observed that the variation in this series is very much less than is found in series of kodaloid discs of similar or even of considerably greater size, when these have been traced on to the kodaloid and then cut from it, as in I (*b*) and III (*a*) and (*b*). This test, therefore, indicates the large element of variability introduced by the manipulations, as compared with the variability due to the substance employed. It demonstrates the importance of introducing all the relevant conditions into a test of accuracy before dependence is placed on a method in further investigations.

III. Test I illustrates probably the method most useful in such observations, namely, the direct tracing of the image on to squared paper. This might seem to be a method specially unfavourable to the accuracy of the kodaloid, on which a secondary tracing was made. (To use kodaloid for the preliminary drawing of a *camera lucida* image is not very practicable.) In many cases, moreover, it is desirable to trace from a drawing or photograph on to the squared paper for measurement. For these two reasons the following series of observations (III) were made. Several more or less circular or oval outlines of different sizes were drawn on cardboard with Indian ink, and of each area twenty-five tracings were made on the squared paper, and twenty-five on the kodaloid. The estimations of area and weight were carried out as before.

Results of Test III

		Average	Standard deviation	Coefficient of variation (%)
III (*a*)	Area (sq. mm.)	4·81 ±0·071	±0·526 ±0·050	10·94 ±1·73
	Weight (mgm.)	1·02 ±0·057	±0·419 ±0·040	41·26 ±4·56
III (*b*)	Area (sq. mm.)	9·50 ±0·115	±0·855 ±0·082	9·00 ±0·865
	Weight (mgm.)	3·37 ±0·042	±0·313 ±0·030	9·31 ±0·895
III (*c*)	Area (sq. mm.)	14·11 ±0·075	±0·554 ±0·053	3·93 ±0·375
	Weight (mgm.)	4·70 ±0·029	±0·213 ±0·020	4·52 ±0·432
III (*d*)	Area (sq. mm.)	20·04 ±0·128	±0·951 ±0·091	4·75 ±0·454
	Weight (mgm.)	6·80 ±0·049	±0·367 ±0·035	5·25 ±0·502
III (*e*)	Area (sq. mm.)	49·89 ±0·173	±1·28 ±0·122	2·57 ±0·245
	Weight (mgm.)	14·77 ±0·079	±0·589 ±0·056	3·99 ±0·381

From Test III it will be seen that as the area increases the liability of both methods to error decreases and that the difference between the variability of the two methods (area and weight) becomes less. At the same time the tediousness of the squared-paper method increases. Therefore under conditions such as these, the use of squared paper, although of great value for the smallest areas, is to be recommended only for these.

The larger squares of squared (coordinate) paper are usually bounded by lines which are thicker than the rest. This inequality in thickness of the lines

would naturally be expected to interfere with the accuracy of the measurements. The actual numerical effect of this was determined as follows.

IV (*a*). Twenty-five areas marked by the metal cylinder on squared paper enclosed thin lines, and only in some instances thick lines also. (This series is the same as the one given under II (*a*) above.)

IV (*b*). Twenty-five areas similarly marked enclosed only thin lines.

IV (*c*). Twenty-five areas similarly marked enclosed always thick lines as well as thin.

Results of Test IV

Series	Average (sq. mm.)	Standard deviation (sq. mm.)	Coefficient of variation (%)
IV (*a*)	5·87 ±0·057	±0·425 ±0·041	7·24 ±0·694
IV (*b*)	6·23 ±0·052	±0·385 ±0·037	6·17 ±0·591
IV (*c*)	5·26 ±0·047	±0·350 ±0·033	6·65 ±0·637

The difference in the coefficients of variation, even between IV (*a*) and IV (*b*), cannot be proved significant because it (1·07) is not even twice the value of its probable error (0·91, obtained by extracting the square root of the sum of the squares of the two probable errors 0·694 and 0·591). On the other hand, the difference between the averages even of IV (*a*) and IV (*b*) (= 0·36) is more than four times its probable error (= 0·077), and therefore the difference is significant: the introduction of thick lines has what may be called an appreciable effect on the average. Hence it is to be recommended that for such small areas perfectly uniform squared paper be used.

SUMMARY

A comparison has been made of two methods of determining the sizes of very small irregular areas, such as photographs or drawings of chromatin particles, of small groups of cells, or of bacteria, or the cerebral convolutions of very small animals—(1) the method of measurement by squared paper, and (2) the method by which pieces of the required shape and size are cut out in celluloid and weighed.

Most of the tests have been designed to reproduce closely the conditions under which actual investigations would be carried out.

The numerical results have been treated by elementary statistical methods.

It has been concluded that for small areas (4 or 5 sq. mm.) the squared-paper method is much the more accurate, and is even less laborious than the celluloid-weight method.

As the areas examined are made larger, the value of the squared-paper method rapidly diminishes.

The inaccuracy of the celluloid method appears to be due principally to the manipulations (tracing and cutting), and not to the substance.

The fact that in most squared paper the larger squares are bounded by

thicker lines than the small squares is of importance, for this lack of uniformity has an appreciable effect on the results in the case of small areas.

Owing to the importance of quantitative methods in these and many other biological problems, the elementary statistical treatment used here has been discussed in some detail.

ACKNOWLEDGMENT

To Dr C. H. Goulden of the Dominion Rust Research Laboratory, Winnipeg, I desire to express my thanks for reading the section of this paper that deals with general statistical methods.

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THE AUSTRALIAN SKULL

By FREDERIC WOOD-JONES
Honolulu

In this paper, which deals with the skull of the aboriginal Australian, I have employed precisely the same methods as those defined in a previous paper dealing with the skull of the Tasmanian (*Journ. Anat.* LXIII, 224).

As in the case of the Tasmanian, I have refrained from attempting to determine the sex of the skulls and the composites are therefore a combination of the skulls of both sexes in unknown proportions.

The basis of the reconstructed composite skull is again the valuable work of Berry, for his excellent dioptrographic drawings of three normae of 90 Australian skulls have been employed. In addition, I have made use of a series of notes and drawings compiled whilst I was in charge of the large collections of skulls in the South Australian Museum and the University of Adelaide. There is no need to recapitulate the methods that have resulted in the recording and treatment of some 40,000 individual measurements that go to the making of these composites of three normae of the 90 skulls.

No attempt is here made to institute a detailed comparison between the Australian and Tasmanian skulls. Any student of craniology is free to do that for himself from the published reconstructions. The present paper aims merely at placing these reconstructed average contours at the disposal of fellow-anthropologists, and forming a basis for instituting comparisons with other races as work develops here.

The contours of the skull are obvious from the figures, and in particular the narrowness of the upper parietal region of the brain-case and the relative facial breadth are conspicuous. Among details it may be noted that the alisphenoid-parietal contact is less extensive than in the Tasmanian, the average contact area being 8 mm. in the Australian against 10 mm. in the Tasmanian. Temporo-frontal contact is not so frequent in this series as in some that have been recorded; but it is often difficult to determine from a drawing if temporo-frontal contact has been actual or has been effected through the intervention of an epipteric bone. Although temporo-frontal contact has been said to be as frequent as 17 per cent. in some series (Duckworth), it would seem that less than half this frequency prevailed in others. Metopism occurs in four cases in Berry's series of 90 skulls. The supra-orbital notch is usually broad and shallow, a true foramen being very infrequent.

As in the case of the Tasmanian skull, the main measurements, as determined in this average of 90 skulls, coincide very closely with Hrdlicka's average derived from nearly 1000 skulls. But, without being led into the temptation of instituting (at present) a comparison with the Tasmanian, it may be said that these composites by no means support Hrdlicka's conclusion that

Fig. 1. Norma lateralis of Australian skull, being the reconstructed average contour of 90 unsexed skulls.

the Tasmanians and Australians "cannot but be regarded as of fundamentally the same race" (*Proc. U.S. Nat. Mus.* vol. LXXI. Art. 24, p. 90, 1928).

As regards cranial capacity, taking the figures from the reconstructed average and using Lee's formula 10 for males, the cubic capacity equals 1308·56 c.c.: by adopting the formula for females, 1271·62 c.c. The mean of these being 1290·09 c.c., which is about the capacity given by several authors.

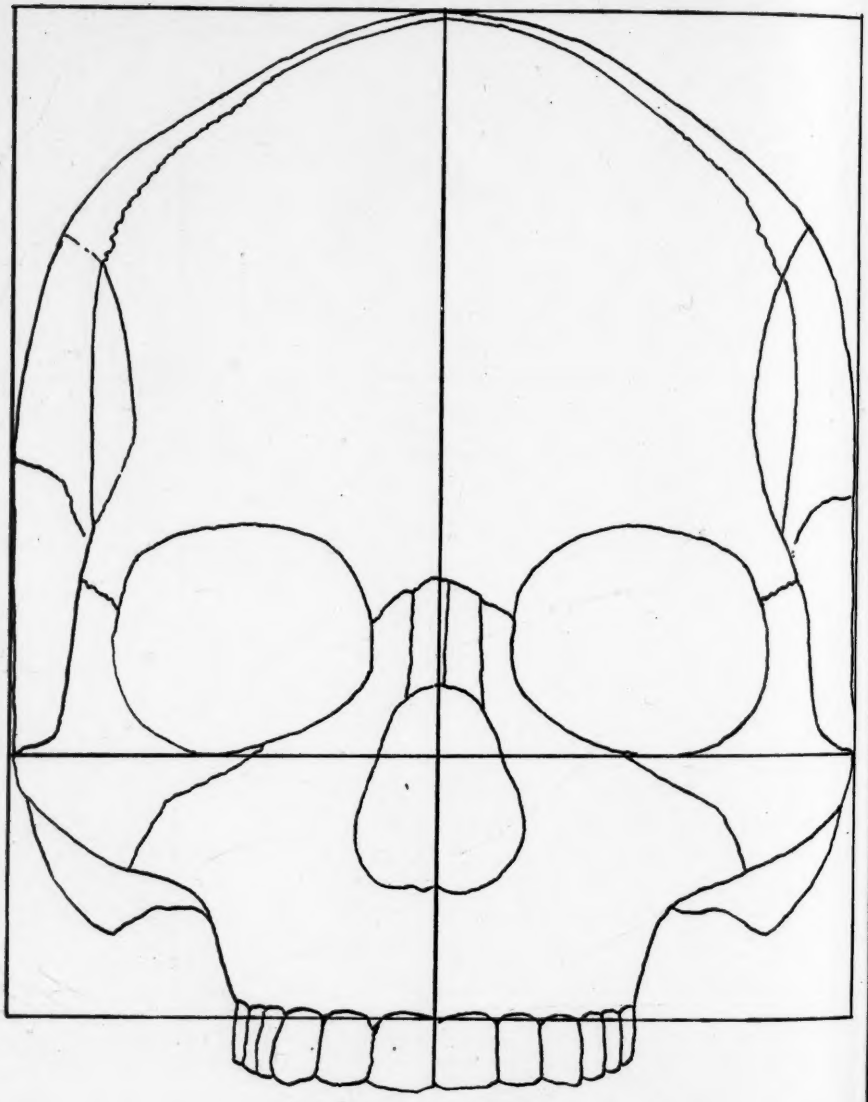

Fig. 2. Norma facialis.

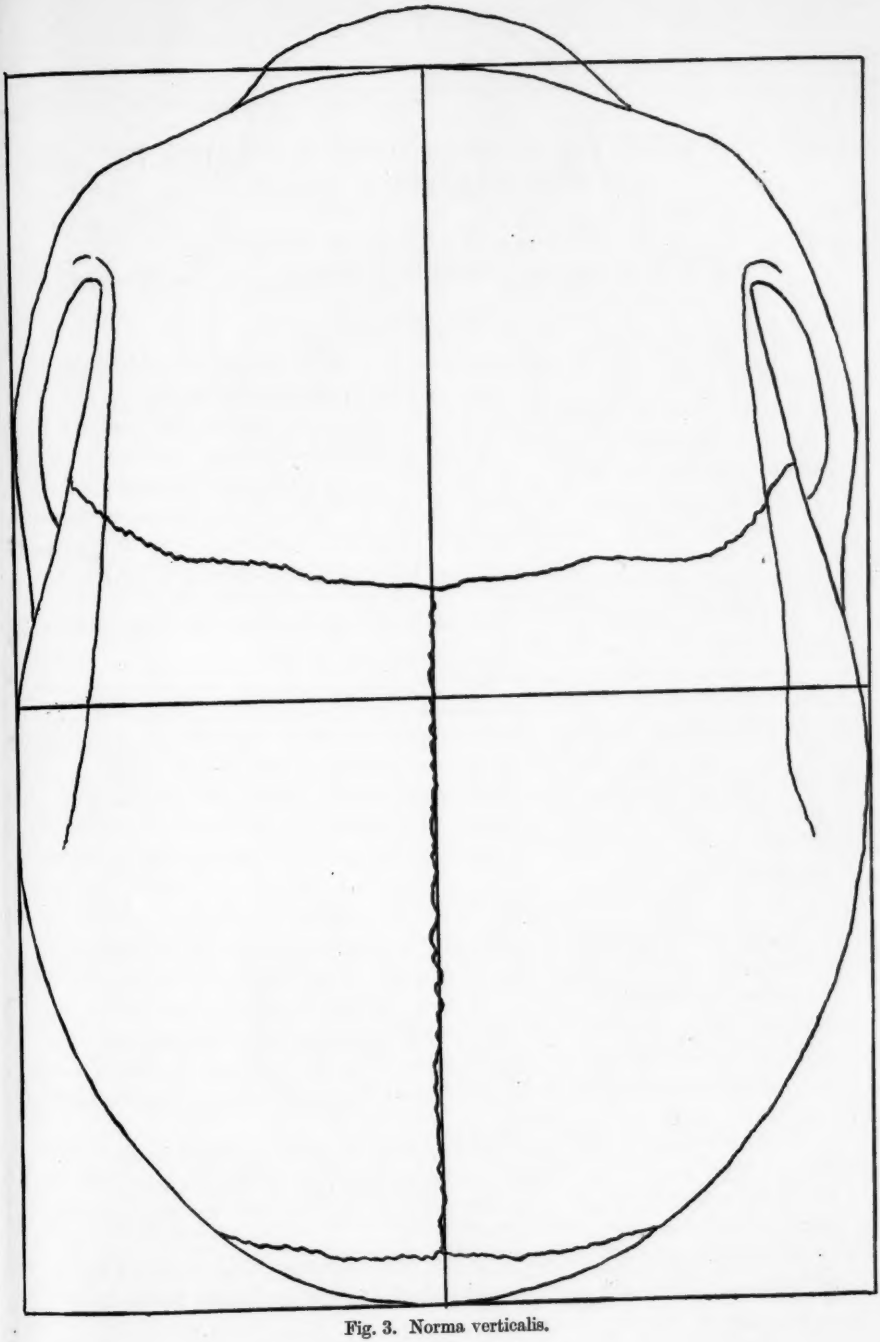

Fig. 3. Norma verticalis.

A NOTE ON SYMMETRICAL THINNING OF THE PARIETAL BONES

By ARCHIBALD DURWARD, M.B., Ch.B.
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INTRODUCTION

In the museum of this department there are now five skulls exhibiting the condition known as "Symmetrical thinning of the parietal bones."

Although Elliot Smith (2) found the condition to be relatively common in Egyptian cemeteries of certain dynasties, the literature does not suggest that to-day symmetrical thinning is at all common. Sir George Humphry (4) had located six specimens in European museums in 1858, and mentioned two others of a doubtful nature. Since that time little has been heard as to the frequency of the condition; but one can hardly suppose that museums possessing large osteological collections can be devoid of examples. Perhaps this reference to "symmetrical thinning" may lead to further information from other sources concerning this very definite, though puzzling, condition.

Examination of about 1000 skulls, both in the dissecting-room and in the museum collection of Maori and Moriori skulls, has yielded five cases of symmetrical thinning—a frequency of approximately 1 in 200. This would appear to be a higher rate of frequency than Humphry had noted in European museums. In 400 Maori and Moriori skulls examined only one case was found. Two of the cases reported belonged to Chinese, but the number of Chinese dissected here, 25 to date, is so limited that conclusions cannot fairly be drawn from this fact.

DESCRIPTION OF CASES

In all cases the process of thinning has operated entirely from without, affecting the outer table and the diploe most constantly. The inner table has, however, been definitely involved in one case (fig. 2) where a perforation has resulted. In no case does the interior of the skull show any abnormality. The condition affects that portion of the parietal between the sagittal suture and the temporal ridge and is about equidistant from both coronal and lambdoid sutures.

The symmetrical nature of the condition is very apparent in all cases, though there may be, as in the skull shown in fig. 3, a difference in the extent of the thinning on the two sides both as to the area of bone involved and the depth of the thinning.

The edges have a characteristic shelving nature so that usually a fairly wide rim of diploe surrounds the central area of exposed inner table. In one

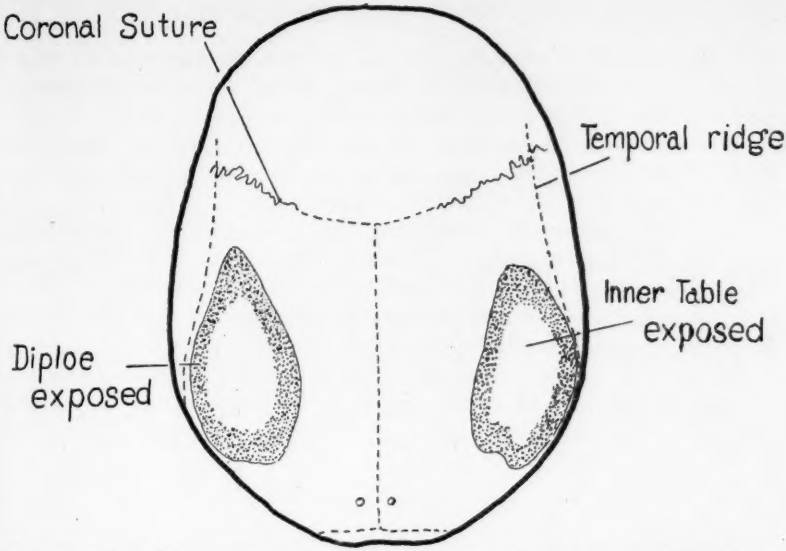

Fig. 1. Skull of a male subject from the dissecting room. The sutures are largely obliterated. The proximity of the thinning to the temporal ridge is evident. The inner table presents a smooth surface compared with the finely nodular surface of the exposed diploe.

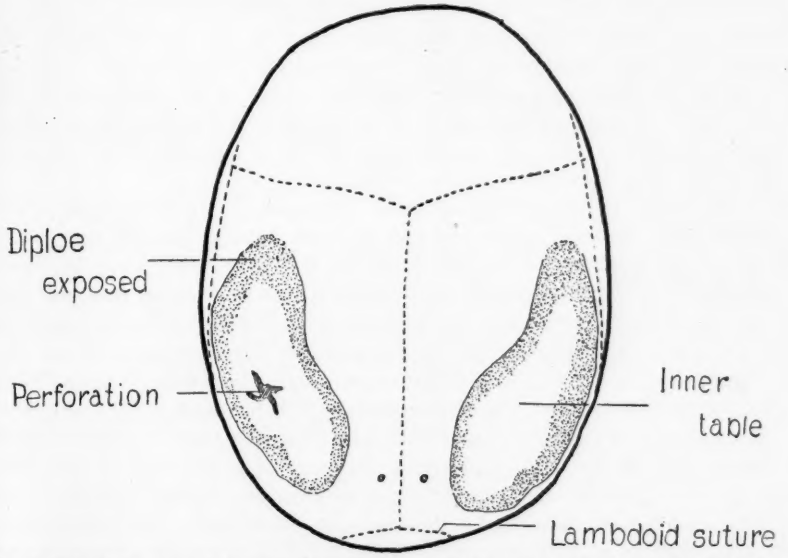

Fig. 2. This skull, removed from the dissecting room, has the sutures almost completely obliterated. Sex not recorded. On the left side the thinning has proceeded so far as to expose the grooves for meningeal vessels in the interior of the skull, an irregular perforation resulting. Other minute foramina exist on both sides leading into the grooves for meningeal vessels.

case (fig. 5), which is somewhat atypical, the shelving nature of the edge is not so apparent and the diploe is not exposed at all, but the symmetrical nature of the condition and its position on the bone are typical.

Both the size and the contour of the areas involved vary very considerably in the different cases of this series, but in every skull the lateral border of the thinned area lies closely against the temporal ridge. In those cases which present a considerable area of thinning (figs. 1, 2, and 3) the lateral border skirts round the temporal ridge in a remarkable manner, and the shelving edge on this aspect is as a rule much steeper than the edge elsewhere. In no case does the thinning extend beyond the temporal ridge, and as shown in the figures the parietal foramina, when present, are not involved.

In the better marked cases the areas of thinning are plainly seen with transmitted light, and where the grooves for meningeal vessels have crossed the field the thinning is very clearly accentuated.

DISCUSSION

Sir George Humphry (4) described the condition briefly in its typical form, mentioning that it is situated midway between the sagittal suture and the parietal eminence, and that the parietal foramina always escape. In this series the areas of thinning would certainly appear to lie nearer the parietal eminence than Humphry found. From the symmetrical nature of the process and from the absence of disease in the specimens he examined, Humphry considered the thinning to be of a congenital nature. He had, moreover, seen a case in a living child, a fact which supported the suggestion of the congenital nature of the condition. In another place (5) Humphry suggested as a possible causal factor the pressure of the occipito-frontalis; but this does not seem likely in view of the very definitely localised areas of thinning.

Elliot Smith (2) had the opportunity of examining over 70 examples of this condition in Egyptian skulls, and from the fact that the thinning was present only in the skulls of the wealthy of certain dynasties when heavy wigs were apparently worn continuously, he concluded that continuous pressure from the exterior, with its resultant interference with the blood supply to the bone, was probably the causative factor. From the skulls he examined he was able to show definitely that the condition was not necessarily a senile one and that both sexes were affected. The thinning appeared to have taken place by erosion of a properly developed cranial wall, and moreover there was not a single instance of its occurrence in an individual under 25, or perhaps even 30, years of age. For the Egyptian cases, then, it appears clear that the condition was not congenital and that it had as its cause continuous pressure from the exterior.

Shepherd (8) also describes the typical form of the condition and records three cases one of which, an adult female, was in the living. In this latter case the evidence pointed strongly to the congenital nature of the condition, and there was a suggestion also of its being hereditary. Shepherd mentions senile

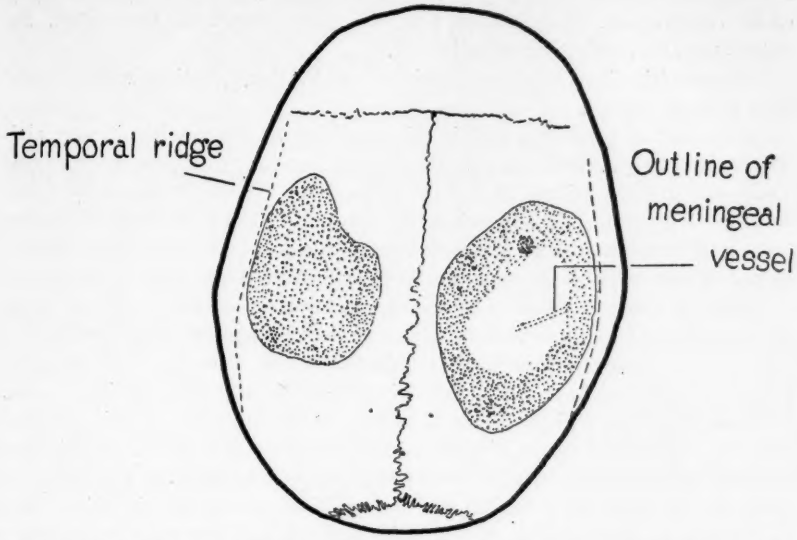

Fig. 3. Skull of a male Chinese, aged 74, from the dissecting room. The sutures are largely obliterated. On the left side the thinning has proceeded no further than to expose the diploe.

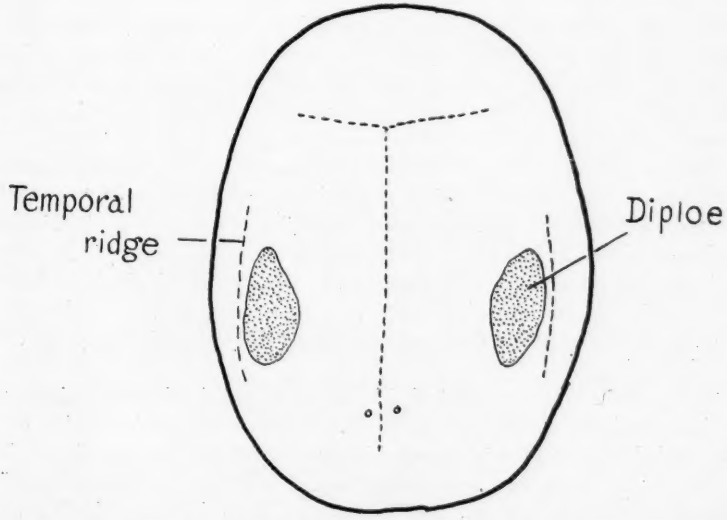

Fig. 4. Skull of a male Chinese, aged 74, from the dissecting room. All sutures closed. The areas of thinning are small and shallow, the inner table being nowhere uncovered.

changes in the temporal artery as a possible causal factor, leading to atrophy of the outer table and the diploe, but leaving the inner table unaffected. He notes that this cannot explain all cases.

The condition is referred to by Maier (6) and Ziegler (9), both of whom regard it as a senile change.

There is the possibility that if this condition be progressive, it may ultimately lead to symmetrical perforations. Greig (3), Derry (1), and Paterson and Lovegrove (7) have written of parietal perforations. While Greig and Derry do not mention symmetrical thinning, Paterson and Lovegrove draw attention to it and state that there is no apparent relationship between symmetrical thinning and such perforation as they described. One skull of the series described in this paper (fig. 2) shows a perforation on one side, but it is not of the type figured by these writers; it has obviously resulted from the thinning process meeting the grooves for the meningeal vessels. Paterson and Lovegrove also state that they have seen symmetrical depressions in foetal parietal bones.

Reviewing the various causes that have been suggested, certain of them may be discounted when applied to the skulls of this series. Continuous pressure from some external object, which adequately explains the Egyptian cases described by Elliot Smith, will not explain the cases of this series where no history of pressure of such a type is forthcoming. Humphry's suggestion of pressure from the occipito-frontalis does not appear to be sufficient in view of the definitely localised areas of bone involved in this series.

It would certainly appear that the condition is most frequently met in aged skulls, and the view that it is really a senile change has had not a few supporters. But Elliot Smith found the condition in relatively young skulls in Egypt; also there are cases on record of its occurrence in the living of such ages that senile changes may be safely excluded; and one skull of this series (fig. 5) is certainly not senile. These facts prove that, though the condition is commonest in advanced life, it is not necessarily a senile change.

Humphry, Shepherd, and Paterson and Lovegrove have all mentioned the likelihood of the condition being congenital, and the former two writers reported cases in the living which were suggestive of being congenital. Though this is not so convincing as the production of the actual skull, yet it must be admitted as a possibility. Elliot Smith did not consider it likely to be congenital so far as the Egyptian skulls were concerned. In view of these facts, then, it must be admitted that, however likely this suggestion may be, direct proof is lacking.

The possibility of symmetrical thinning of the parietal bones being a progressive condition appears not unlikely. The most constant position of the thinning is just above the temporal ridge and about midway from before back on the bone. From this spot spread would take place forwards, medially towards the sagittal suture, and backwards, and also the thinning would become progressively deeper. This would account for the varying areas of thinning met in different skulls. The constant proximity to the temporal ridge

seems certainly to have some significance. The blood supply to the bone would be assured from the level of the temporal ridge downwards owing to fascial and muscular attachments, whereas above this level the nourishment of the bone would not be assured by any such attachment. The possibility exists therefore that the condition may be progressive and that it may depend upon some deficiency in the blood supply. No cause for this deficiency which would account for all the cases of this series is evident.

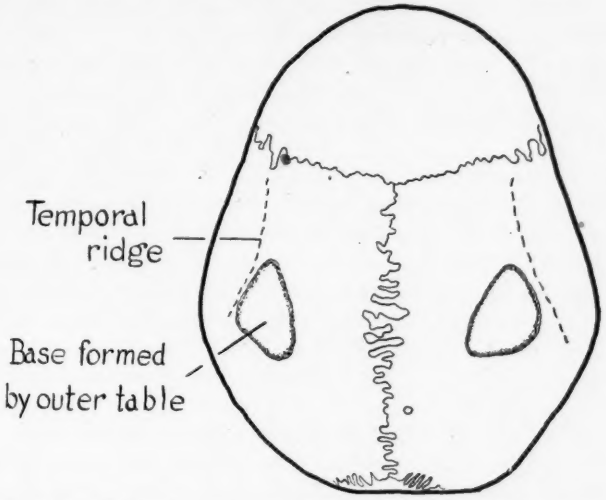

Fig. 5. Maori skull with all sutures open; over 25 years of age. The diploe is not exposed and the edges are not so typically shelving as in the other cases.

SUMMARY

1. Five cases of symmetrical thinning of the parietal bones are described.

2. The literature available is briefly reviewed and existing theories as to causation are mentioned.

3. The constant proximity of the thinning to the temporal ridge in the cases of this series is stressed.

4. It is suggested that the condition may be progressive, and that it may be caused by a deficiency in the blood supply to the bone above the level of the temporal ridge. No cause for such deficiency is suggested.

In conclusion I wish to express my thanks to Prof. W. P. Gowland for permission to publish the cases which have occurred in the Museum and in the dissecting-room of this department.

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A NOTE ON THE ORIGIN OF PANCREATIC BLADDERS

By EDWARD A. BOYDEN, Ph.D.
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The exclusive occurrence of pancreatic bladders in the domestic cat has interested students of embryology ever since F. T. Lewis made the tentative suggestion in correspondence with Miller and Dresbach, that "pancreatic bladders are extreme cases of subdivided hepatic diverticulum,—that is, they are cases of double gall-bladder, emptying into a subdivided cystic and common bile duct." (Dresbach, 1911, p. 369.)

Since then, in opposition to a still earlier view that stressed an origin from the ventral pancreas (Miller, 1910), two new hypotheses have been advanced: first, that the pancreatic bladder represents the caudal half of the primary liver diverticulum—the latter being an organ of dual potentialities (Bremer, 1923); and second, that it is as much intestinal in origin as pancreatic or hepatic,—an anatomical sport induced by some hypothetical physiological deficiency occurring at the critical moment of origin of the liver bud and "readily explained in terms of a developmental arrest" (Bean and Dreyer, 1927 b).

Previous to the latter article the writer had shown that the pancreatic bladder is more common than had hitherto been recognised—five cases having been found in approximately 2600 cats; and that since at least one case existed in which a pancreatic bladder arose directly from an accessory pancreas of the lower duodenum (1922), the problem became whether there were two different origins of pancreatic bladders, or whether all of them were outgrowths of pancreatic tissue. In support of an exclusively pancreatic origin it was then shown that in these 2600 dissections no bifurcated biliary tracts had been observed that were intermediate in type between cleft gall bladder and pancreatic bladder; that numerous instances of accessory lobes of pancreatic tissue had been found which not only extended to the fossa of the gall bladder but duplicated all known types of pancreatic bladder in their method of attachment to the pancreas; and that in all cases examined, the two vesicles were different histologically—the mucosal pattern of the pancreatic bladder being referable to that of a pancreatic duct (Boyden, 1925).

Such was the situation when Bean and Dreyer (1927 b) reported a unique case of double pancreatic bladder consisting of a large vesicle, to the neck of which was appended a smaller one. Since the common duct of these pancreatic bladders arose directly from the tissue of the ventral pancreas at as great a distance from the ampulla of Vater as 20 mm., the case could not be explained on the basis of subdivision of an hepatic diverticulum having dual potentiali-

ties. But because the smaller of the two pancreatic vesicles seemed to resemble a gall bladder, Bean and Dreyer felt obliged to deny the pancreatic origin of both vesicles, even though these were attached to the pancreas and although the mucosa of the larger one duplicated the case described by the writer as resembling an hypertrophied pancreatic duct. Hence the resort to the physiological explanation described at the beginning of this article.

However, in reviewing the two cases described by these authors, the writer is not impressed by the necessity for a new theory. Without voicing the many objections that could be raised against their hypothesis, it may well be asked whether the smaller lobe of this double pancreatic bladder is a true vesica fellea. Fig. 13 of Bean and Dreyer's article would seem to afford conclusive proof that it is not. For, notwithstanding its apparent resemblance to the gall bladder, the left upper quadrant of this vesicle contains two clusters of glands that have penetrated the tunica muscularis. As such glands do not occur in the gall bladder of the cat, this clearly identifies the organ with the pancreatic bladder, in addition to which there is the authors' statement that the duct of the smaller vesicle resembles the main duct of the pancreatic bladder. Accordingly, the appended vesicle may be interpreted as an accessory ductular pancreatic bladder, comparable to the small ductular gall bladders that frequently bud out from the peripheral bile ducts of the cat (Boyden, 1926, fig. 2).

A similar doubt regarding the histological nature of the pancreatic bladder seems to have confronted Bean and Dreyer in the first case that they found (1927 a). Since that pancreatic vesicle also superficially resembled a gall bladder, they concluded that it must have originated by subdivision of the embryonic hepatic diverticulum. But in establishing the criterion of histological differentiation the writer had been confronted by the same problem, and after modelling that case which resembled a gall bladder as much as Case 1 of Bean and Dreyer (Boyden, 1925, fig. 15), he was able to establish two critical differences—namely, the existence of a more delicate rugose pattern in the pancreatic bladder; and the occurrence of clusters of tubulo-alveolar glands that differed markedly from the basal crypts of the gall bladder (fig. 22, *l.c.*). From a study of the figures in Bean and Dreyer's first article there is little doubt but that these authors were deceived by the distended condition of this vesicle and that if they had modelled it they would have found as striking differences as the writer found in Case 7 of his own series.

The second specimen (1927 b) confirms this suspicion, for the larger vesicle closely resembles a collapsed pancreatic bladder described by the writer (Case 5). Evidently Bean and Dreyer realised this for they abandoned the theory that pancreatic bladders originate by subdivision of an hepatic diverticulum having dual potentialities. But surely these authors are in error when they state that the primary vesicle of Case 2 resembles intestinal tissue, or the duodenum (as designated by the new edition of Babkin's excellent textbook (p. 453)). To be sure, occasional villi, containing vascular and lymphatic

plexuses, do occur in both the gall bladder and in the pancreatic bladder—at the intersections of the folds—but the primary pattern of these vesicles is rugose and not villose, as in the small intestine. Beyond doubt some of the structures labelled villi (in Plate II) are really transverse sections of rugae, and argue against the theory that pancreatic bladders resemble the intestine. By the same token there are no short cylindrical crypts of Lieberkuehn, such as occur in the small intestine. This is apparent in figs. 10 and 12 of their second paper. Also it is obvious that the relative proportions of the elevations and depressions of the mucosa are very different from those in the small intestine of the cat. Finally in both the pancreatic bladder and the gall bladder the tunica muscularis lies directly against the tunica propria—for which reason it has been defined as an enlarged muscularis mucosae (Pfuhl, Halpert). Indeed, one would never mistake either the pancreatic bladder or the gall bladder for the small intestine.

Nevertheless, the fact remains that in some cases the pancreatic bladder so closely resembles the gall bladder as to have been confused with that organ, whereas in other cases its mucosal pattern is such as to have caused it to be compared with the intestine. How may these extreme types be reconciled? Merely by showing that they have the same intrinsic pattern and that the second type is a modification of the first. Type I is a distended pancreatic reservoir. Its resemblance to the gall bladder is as close as the resemblance between the pancreatic ducts and bile ducts to which the respective vesicles are attached. Judging from its distension and position (in the fossa vesicae felleae) this type of pancreatic bladder has developed under the same mechanical conditions as the gall bladder. As examples of this type may be cited Cases 1 and 2 (small vesicle) of Bean and Dreyer; Cases 4 and 7 (Boyden 1925, Plate II). The second type (Cases 2 and 9 of the author) represents a contracted pancreatic bladder in a condition of extreme hypertrophy. Proliferation of the epithelium has resulted in exaggeration of the primary rugose pattern and has produced a thick tunica mucosa, with wedge-like folds projecting into the lumen (fig. 3), each wedge telescoped by numerous subsidiary folds (fig. 1) from the base of which emerge great numbers of slender glands (figs. 1 and 2). An intermediate stage of hypertrophy is illustrated by Case 2 of Bean and Dreyer (large vesicle); and by Case 5 (Boyden, 1925). Obviously it is not the province of this article to supply the reasons for this hypertrophy, but contemplation of possible factors affords an interesting field for speculation.

In conclusion, it may be stated that although the considerations which have led Bean and Dreyer to reject the natural theory that pancreatic bladders are aberrant outgrowths of the ventral pancreas do not seem to be justified, nevertheless their account of a double pancreatic bladder constitutes an important contribution to the subject and emphasises, once more, the extraordinary capacity for variation exhibited by the organs of the porta hepatis.

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DESCRIPTION OF PLATE

PLATE I. Photomicrographs of the pancreatic bladder of a cat. (Case 9, November 7, 1928; in gross appearance, this specimen resembled Case 5, previously described.)

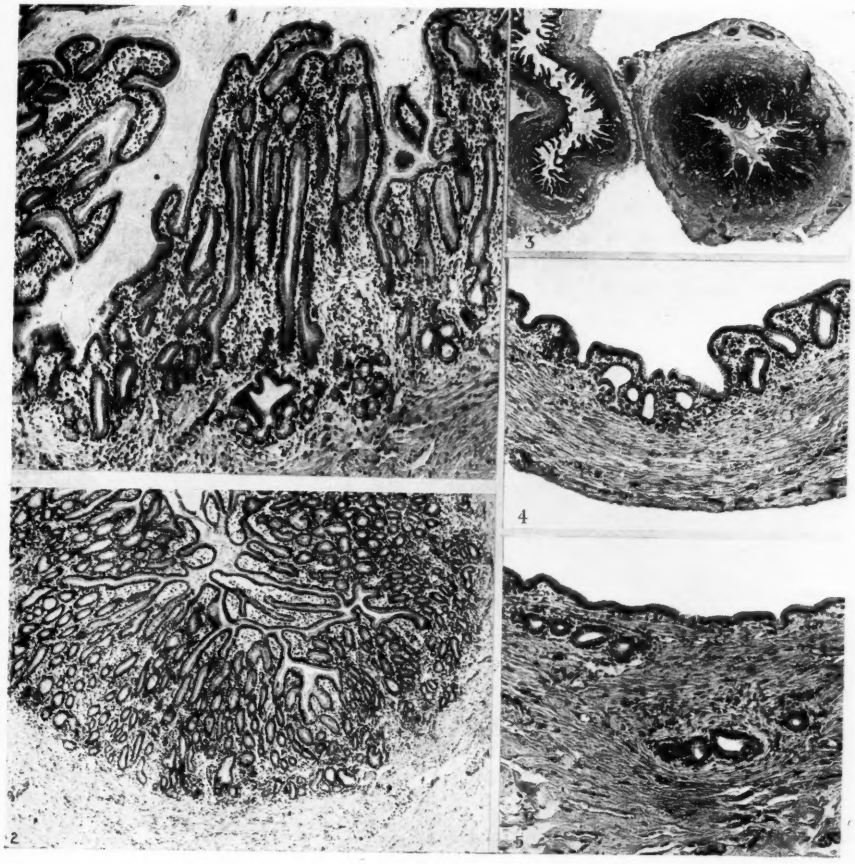
Fig. 1. Detail of wedge-like areas of the mucosa similar to those seen under low power in fig. 3 (right). Note telescoping of wedge by its constituent folds; and the clusters of glands at base of wedge. ×60.

Fig. 2. Tangential section of fundus of pancreatic bladder, showing the rugose pattern of the mucosa. ×40.

Fig. 3. Low-power view of gall bladder (left) and accompanying pancreatic bladder (right), lying in fossa vesicae felleae. Note mucosal, muscular, perimuscular and serous tunics; and the extension of some glands into the tunica muscularis (cf. fig. 5). ×8.

Fig. 4. Cross-section of cystic duct of pancreatic bladder in a region showing its rugose pattern. ×60.

Fig. 5. Another area of the cystic duct of the pancreatic bladder, showing the extension of glands into the muscular tunic. The duct of Case 9 emptied into the splenic division of the ductus pancreaticus at exactly the same place as that of Case 5 (fig. 11, Boyden, 1925). ×60.



UNIV. OF MICH.

THE DISTRIBUTION OF THE FIRST INTERCOSTAL NERVE AND ITS RELATION TO THE FIRST RIB

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The object of this paper is to attempt to indicate the course and distribution of the first intercostal nerve with more precision than the text-books are accustomed to allow, and to demonstrate how this nerve is responsible for the presence, on the under surface of the first rib, of certain grooves or markings, hitherto undescribed, and not figured, to my knowledge, in any osteology. It will further be shown that this nerve, in the disposition of its branches, furnishes a key to the correct interpretation of the morphology of the brachial plexus, whilst its relatively exposed position in the subpleural connective tissue of the thoracic operculum invests it with a certain clinical interest in connection with inflammatory conditions of the upper thorax.

In the determination of the cutaneous distribution of the first dorsal nerve, either by gross dissection or by clinical study, most attention in the past has been naturally focussed upon that part of D. 1 joining the brachial plexus, not only because it is this portion of the nerve which is involved in cases of pressure from a cervical or from a normal first rib, but also because the large area of skin supplied by this portion affords a clue to the diagnosis of lesions of the first thoracic cord segment. Thus it happens that most anatomical authors whilst describing carefully the plexal portion of D. 1 have generally much neglected its intercostal portion, dismissing it usually with the statement that it "gains the first intercostal space," and either denying it anterior and lateral cutaneous branches, or suggesting that such branches are present only occasionally. Much of the current teaching attributes to the supra-clavicular branches of the cervical plexus the office of supplying skin down to the level of the second rib, although such a supply is not the rule, and if it ever occurs, is the exception. The "overlap" of these descending cervical branches, together with the narrow (sometimes almost linear) extent of the skin area supplied by N. intercostalis 1 may render somewhat difficult the clinical determination of the cutaneous distribution of the latter nerve.

Recently, however, in a case of lesion of the first thoracic cord segment in which, among other symptoms, there was anaesthesia over the distribution of D. 1, I have been able to satisfy myself as to the existence and extent of the cutaneous distribution of the first intercostal nerve, and find that it supplies skin over an area covering the first intercostal space, upper part of the second rib, the anterior axillary fold and axillary floor as far as the area supplied by

Wrisberg's nerve. Therefore D. 1 supplies a continuous zone or skin strip from the mid-thoracic line ventrally, along the ventral axial line (by its intercostal portion) to the post-axial border of the upper limb (supplied by its plexal portion).

Notwithstanding this fact, Quain's *Anatomy* (1) definitely states that "the first thoracic does not give any branches to the skin of the trunk with the exception of a small area on the dorsal surface near the spine" although a diagram of the segmental cutaneous areas (based on Head's researches) is given on the previous page, wherein the first thoracic is indicated as supplying skin on the front of the chest. Similar diagrams from other sources show interruption of the continuity of the first thoracic spinal dermatome by the inthrust of the second thoracic nerve and its intercosto-humeral branch to the skin of the arm; the presence of a lateral cutaneous branch from the first intercostal is overlooked, yet such a branch is constant and supplies a definite strip of axillary skin.

A brief survey of the standard texts emphasises the neglect accorded to the intercostal nerves in general, and to the first intercostal nerve in particular. Its course and relations are briefly dismissed, and its various branches advanced with a certain degree of dubiety.

Joseph Swan (2) in 1834 described the first intercostal as "giving a filament to the great pectoral muscle and communicating with filaments from the third cervical nerve passing over the clavicle" and then terminating cutaneously. An "external branch" (= lat. cut.), also described, communicated with Wrisberg's nerve and replaced that nerve, supplying skin "at the posterior and inner side of the arm as far as the elbow."

D. J. Cunningham (3) in 1879 definitely stated that the first intercostal, "although disposed after the manner of an intercostal nerve, furnishes no lateral cutaneous branch," a statement repeated by Turner (4) in 1882. Indeed, these two anatomists appear to be responsible for the traditional absence of a lateral and an anterior cutaneous branch from intercostal 1, a tradition maintained in the latest (8th) edition of *Practical Cunningham* (5), wherein it is said (p. 11), "the first intercostal nerve does not give a lateral cutaneous branch. Nor does it become cutaneous at its termination."

Piersol (6) is self-contradictory. He says, "Each of the thoracic nerves, with the exception of the first, sends out a lateral cutaneous branch, and with no exceptions, an anterior." The anterior branches are "constant in arrangement and distribution with the exception of the first, which is very small or absent," whilst a first thoracic "lateral cutaneous branch is rare."

Macalister (7) is silent on the matter. A. Soulié (8) carefully describes the course of N. intercostalis 1, but omits a ventral termination in skin, and regards a lateral branch as "fort rare," remarking that Valentin, however, found such a branch, communicating with intercostohumeral.

Testut (9) follows Schwalbe in identifying the first thoracic lateral cutaneous branch with those fibres of D. 1 which cross the first rib in the brachial plexus,

to reach skin through the internal, or the lesser internal, cutaneous nerves; and he considers the nerves of the plexus to be cervical lateral branches, rather than cervical anterior primary divisions.

In view of the discrepancies and doubts expressed in the literature, investigation of the first intercostal nerve was undertaken in the dissecting room and autopsy theatre. Simultaneously Mr F. H. Bentley, B.Sc., also investigated this nerve in the course of some research work under Prof. Stopford at Manchester, and he has kindly allowed me to incorporate his findings—which confirm those obtained in the Leeds Department—in this paper.

MATERIAL

Careful dissection was performed bilaterally in 30 adult dissecting room subjects (12 by Bentley in the Manchester Anatomy Department, and 18 here) and 10 foetuses (6 full term, and 4 of ages varying from 5 months to term). A large series of dissections was carried out in the post-mortem room of the Leeds General Infirmary, the preliminary observations on the origin of twigs being confirmed by a more leisurely and complete investigation of the whole root of the neck and thoracic operculum removed in its entirety for this purpose. For nerve markings, 190 first ribs were examined; 75 modern bones in this Department, 32 modern bones in the Manchester Anatomy Department, and from the same source 83 Ancient Egyptian ribs. These last, so Professor Elliot Smith kindly informs me, are from burials covering a very wide range in time, and, irrespective of age, the material is of the Proto-Egyptian type. Certain specimens in this ancient series were from a cemetery of the sixth century A.D., found in the island of Hessa, immediately above the First Cataract: these people were Nubians "but the type of the people is essentially that of the predynastic Egyptians" (10). Two pairs of Gorilla, and four pairs of Chimpanzee, first ribs were also examined.

COURSE OF THE FIRST INTERCOSTAL NERVE

In the lower ("typical") intercostal spaces the intra-costalis muscle (Walmsley) is well developed, and the intercostal nerve runs between this muscle and the internal intercostal, giving off a collateral or long muscular branch which, running between the internal and external intercostal muscles, largely or entirely expands itself in the innervation of the latter muscle. In the uppermost two spaces, however, the intra-costalis is deficient, being represented by a few fibres only in the second space and being absent usually from the first. (I am not here concerned with those muscle fibres which continue the scalene musculature into the first space, and are so evident in the foetus and new-born.) Hence the typical relationship of intercostal nerve to intercostal musculature is, in the first space, departed from: absence of the intra-costalis

causes the first intercostal nerve to lie, for the greater part of its course, internal to the muscles of its own space, and it can be readily exposed by stripping up the parietal pleura. The nerve is literally "intercostal" in the last part of its course only.

As D. 1 reaches the medial border of the first rib, it gives off the first intercostal nerve, which, running obliquely outwards behind the insertion of the anterior scalene, crosses the under surface of the rib in its middle portion, to gain the first intercostal space at about the junction of the rib with its cartilage.

So far, the nerve (*A* in fig. 1) is in intimate contact with the inferior surface of the first rib, bound thereto by a local thickening of the endothoracic-fascia, and in about 60 per cent. of cases producing a mark or a groove (*sulcus diagonalis*) on the bone. Having gained the ventral end of the first space, the nerve continues its forward sweep, first on the medial aspect of the internal intercostal, later in the substance of that muscle, supplying it the while with numerous fine twigs. Approaching the sternum, it emerges from the internal intercostal to lie again in the subpleural tissue for a short distance, then, crossing the internal mammary vessels, it turns forward through the chest wall (accompanied by a small branch from those vessels) to terminate as the first thoracic anterior cutaneous nerve. As such, it is distributed to the skin over the first intercostal space and the upper border or more of the second rib, for a variable distance. Occasionally it extends on to the skin of the arm, crossing the anterior axillary fold, and in such instances the lateral cutaneous branch of N. intercostalis 1 is very small; occasionally, also, it communicates by fine filaments with the descending cervical nerves, as Swan observed. Before becoming cutaneous, the first intercostal nerve gives most of its twigs to the internal intercostal muscle, but sometimes a long slender filament (*P* in fig. 1), having a variable origin from the nerve, is distributed to the periosteum on the back of the manubrium sterni and angulus Ludovici.

At the point of origin of the first intercostal nerve, a long thin branch (*B* in fig. 1) arises, passes almost horizontally outwards, pierces the internal intercostal to run between that muscle and the external, and expends itself in the supply of the latter. This constant branch, corresponding to the collateral muscular branch of the lower spaces, is frequently responsible for another groove (*sulcus transversus*) or marking on the inferior surface of the first rib.

Another constant branch (*C* in fig. 1) arises at the origin of the first intercostal nerve and turns backwards through the posterior wall of the space to end in the substance of the serratus posticus superior. A lateral cutaneous branch (*L.C.* in fig. 1) is invariably furnished by the main trunk of the first intercostal: it pierces the chest wall in front of the first digitation of the serratus magnus and in the line of exit of the intercosto-humeral, to be distributed to skin of the mid-axillary line in front of the axillary vessels. Though generally small, its size varies somewhat, usually in inverse proportion to that of the first anterior thoracic. Bentley found this lateral branch bilaterally in all his

twelve subjects; in this Department it was absent occasionally (once bilaterally, and four times on one side or the other) owing to dissection of the axilla by students. In the post-mortem room it was secured at its origin by dissection of the first space from the internal aspect, and then traced out more fully by a subsequent axillary dissection.

In about 25 per cent. of cases, this lateral cutaneous of the first intercostal joined the nerve of Wrisberg; in two cases wherein, bilaterally, Wrisberg's nerve was a mere delicate thread, the first lateral cutaneous joined with it and then replaced it, supplying skin down to the elbow, as in Swan's instance. The intercosto-humeral in these two cases appeared smaller than usual. Bentley

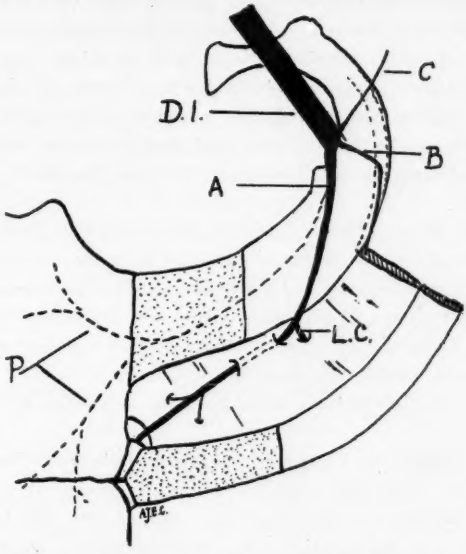

Fig. 1. Course and branches of N. intercostalis 1: *A.* = main nerve; *B.* = its collateral muscular branch; *C.* = its posterior muscular branch; *P.* = periosteal twig; *L.C.* = lateral cutaneous branch.

and I each observed one case of the lateral cutaneous crossing the axilla to join Wrisberg's nerve in conjunction with an intercosto-humeral of normal size. In about 25 per cent. of cases, the first and second lateral cutaneous nerves communicated on the side of the chest, the loop so formed frequently receiving a filament from the third nerve of the lateral series.

MORPHOLOGY OF BRACHIAL PLEXUS

It should be noted that Wrisberg's nerve was present in every case dissected and had the above-mentioned relations to the first lateral cutaneous. Since the latter nerve is a constant feature of human anatomy, the lesser

internal cutaneous cannot be, as Schwalbe and Testut imply, the homologue of a thoracic lateral nerve, and I cannot agree with Wilson's(11) statement that "in man, as in the typically mammalian brachial plexus of the porcupine, the lateral cutaneous nerve of the thorax" is Wrisberg's.

Utilising the transitional character of the first dorsal nerve to elucidate the morphology of the brachial plexus, certain authorities (e.g. Goodsir, Thane, Symington) would regard the plexal portion of D. 1 as a lateral cutaneous nerve, and by analogy interpret the roots of the plexus as cervical lateral nerves, the scalene twigs being regarded as the modified ventral rami.

It is obvious that the brachial nerves represent something more than cervical lateral cutaneous branches. The lateral cutaneous branches of C. 2, 3 and 4 are distributed to the skin of the cervical portion of the trunk, those of D. 2, 3, 4, etc., to the skin of the thoracic portion; the lateral cutaneous branches of C. 5, 6, 7 and 8 are dragged out to the skin of the upper limb, through the brachial plexus. Since the first dorsal spinal segment gives a contribution both to the trunk and to the limb, the first dorsal ventral ramus is compelled to divide into axial and appendicular portions for the innervation of its own particular tissue.

The plexal portion of D. 1, therefore, in common with C. 5, 6, 7 and 8, consists of a lateral cutaneous branch to arm skin *plus* something more—i.e. plus the motor fibres passing out to innervate the limb musculature. Like the lower cervical nerves, it gives off cutaneous branches (Wrisberg's nerve, etc.), but is not itself wholly sensory. (The thoracic portion of D. 1 falls into line with the upper cervical and remaining thoracic ventral rami, having a typically segmental distribution, and like them, providing a lateral cutaneous branch.)

Thus, the brachial nerves consist of lateral cutaneous branches together with motor fibres: they represent the whole of their ventral rami, and give support to the opinion of Paterson, Eisler, and others, viz. that the brachial plexus nerves are cervical anterior primary divisions (not lateral branches) and that the scalene offshoots are merely muscular twigs. This interpretation is more in accordance with the anatomy of the deep cervical region, as evidenced by the morphology of the inter-transversarii and scaleni.

The first dorsal nerve, situated caudally in the brachial plexus, has its own peculiar distribution, as determined by the embryological fate of the mesoderm of its own spinal segment: it is therefore compelled to follow this tissue, partly into the somatopleure and partly into the forelimb. Its plexal portion should not, therefore, be regarded as a lateral nerve, but as a special nerve meeting exceptional developmental requirements, a subdivision (like the first intercostal) of the first thoracic ventral ramus. Indeed, it is only the assumed absence of a lateral cutaneous branch from N. intercostalis 1 that has dwarfed the significance of the splitting of the first ventral ramus into intercostal and brachial portions, and obliged the latter portion to assume the rôle of a lateral branch.

THE GROOVING OF THE FIRST RIB

Both the main branch of the first intercostal nerve and its collateral muscular branch may produce grooves or markings on the first rib, such impressions varying considerably in their actual features. Typically, two grooves, a diagonal and a transverse, are present, but a single, diagonal groove may alone occur. Sometimes a common groove near the medial border of the rib forks into the two typical sulci; once only, I encountered an adventitious sulcus (Egyptian rib, No. 40 R.) due to the retro-sternal periosteal branch of the nerve.

The grooves are frequently wide rather than deep (in conformity with the flattened nature of the first intercostal nerve): they may be deep and obvious, but all varieties of distinctness may be observed down to a mere smoothing or texture-difference of the bone where the nerves lie in contact with it. Often the sulci are very distinct at the medial border, but fade away as traced across the bone, although, equally, they may remain quite pronounced up to the outer border of the rib. (When faintly marked, the grooves are rendered more obvious by slightly wetting the bone's pleural surface.)

The frequency of their occurrence is shown in the following table:

Table I.

Department	*No. of bones examined*	*With grooves or markings*
Leeds	75 (R. 36. L. 39)	69·2 %
Manchester	32 (R. 13. L. 19)	80·0 %
Manchester (Egyptian)	83 (R. 43. L. 40)	57·0 %
Total	190 (R. 92. L. 98)	Average = 68·7 %

The figures for the Ancient Egyptian series are probably somewhat low, the bones having been exposed to the weathering action of sand and other agents. Table II shows that the right first rib was more frequently grooved, in all three series, than its fellow of the left side.

Table II.

Type of Bone	*Right First Rib showing Sulci*	*Left First Rib showing Sulci*
Modern	69 %	62 %
Ancient Egyptian[1]	62 %	61 %

The relation of the sulci on the under surface to the *sulcus subclaviae* (B.N.A.) on the upper surface of the first rib was also investigated. It was found, firstly, that the *sulcus subclaviae*, which is usually regarded as a constant feature of this bone, was definitely present in but 50 per cent. of specimens, being doubtfully represented in a further 30 per cent., and completely absent

[1] The percentage figures for ancient Egyptians in Table II were based on an examination of 73 first ribs only. This explains the slightly higher figures in Table II as compared with that in Table I.

in the remaining 20 per cent. Thus the diagonal and transverse sulci have as good a claim to recognition as a normal characteristic of the first rib, as has the subclavian sulcus. Secondly, in first ribs with absent *sulcus subclaviae*, the grooves described are definitely present in 50 per cent. of such specimens, are faintly indicated in a further 25 per cent., and are absent from the remainder.

It was observed that ribs of the thin, "flat" type best exhibited these markings, which were absent from bones having an oval or round cross-section. Hence, the thick, rounded and robust gorilla ribs showed no evidence whatsoever of nerve markings, upper and lower surfaces being practically indistinguishable. Chimpanzee first ribs also yielded no sign of inferior grooving, but a much larger series of anthropoid first ribs requires scrutiny before a definite opinion can be expressed concerning the absence of nerve impressions as a typical feature of such bones.

CERVICAL RIB AND RUDIMENTARY FIRST RIB

In cases of cervical rib, when a "highest" intercostal space is present, its innervation is derived from C. 8 or D. 1, but I know of no mention of any nerve groove on the under surface of a cervical rib, although such a groove might well be expected in those specimens of cervical rib which continue an uninterrupted course forward and articulate with the sternum or first costal cartilage. Wingate Todd (12) has shown, from dissections of cervical rib, that in these cases the nerve supply of the space between the first and second dorsal ribs is derived always from D. 1, the intercostal nerve of that space being disposed apparently after the manner I have described above as normal: for Todd says it "formed two small twigs" (? main nerve and collateral muscular branch), the uppermost twig being associated with an ill-defined groove on the under surface of the first (dorsal) rib. He mentions no lateral branch, nor does he anywhere appear to regard the grooves mentioned as normal features of the first dorsal rib. It would thus appear that in cervical rib, the disposition of the nerves in the space between the first and second dorsal ribs is of normal type, and this is confirmed by examination of an example of bilateral cervical ribs in this Department. The specimen consists of vertebrae C. 6, 7 and D. 1 with the two cervical and the two first dorsal ribs. On the right, the cervical rib is fused with the seventh vertebra, and the first dorsal rib shows well-marked diagonal and transverse sulci on its lower surface. On the left, the cervical rib is free; it articulates with the body and transverse process of the seventh vertebra by its head and tubercle respectively, whilst the knobbed and facetted extremity of its short shaft articulates with an upstanding bar of bone from the medial border of the first dorsal rib of that side. The under surface of this rib exhibits a faint groove which rapidly bifurcates into very well-marked diagonal and transverse sulci (see fig. 3). The *sulcus subclaviae* is absent bilaterally.

When the first dorsal rib is rudimentary, the second thoracic nerve tends

to assume the course and distribution typical of the normal first nerve. Wood Jones (13) has depicted the gross relation of nerve to rib in one such case, making no mention, however, of grooves, nor of collateral and lateral branches

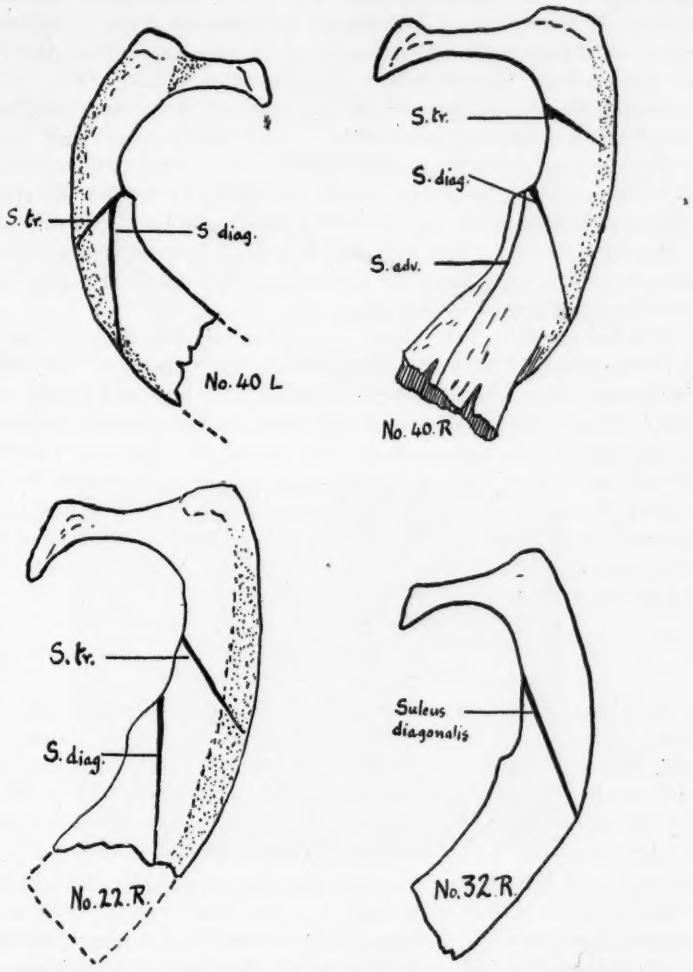

Fig. 2. Ancient Egyptian first ribs, illustrating variations of the sulci on the inferior surface.

of the second thoracic nerve. Rutherford Dow's two cases (14) of rudimentary first rib demonstrated this assumption by the second thoracic nerve of the normal characters of its cephalic neighbour, but again no details are available concerning branches from the nerve or rib grooving.

Todd, however, in dissecting a specimen of reduced first rib (subject C in his account) wherein on each side the first complete rib had "the characteristics of a normal second dorsal rib," observed that "the under aspect of both these ribs is grooved for the intercostal nerve," which nerve came from the second thoracic. In a specimen of left rudimentary first rib in this Department, the highest costal arch on the left is formed by the second dorsal rib with which the first rib has fused immediately beyond its tubercle and behind the line of crossing of the brachial nerves: the under aspect of this arch exhibits an ill-defined *sulcus diagonalis* and a better marked *sulcus transversus*. Both sulci are due, presumably, to the second thoracic nerve, although no certain opinion can be expressed in the absence of the soft parts. (A normal first rib, devoid of nerve markings, forms the uppermost costal arch on the right.)

It seems, therefore, that when the first rib is rudimentary, the second rib may assume the characters of the normal first rib, even to the acquisition of the nerve markings proper to that rib.

Dow has questioned the authenticity of certain reported cases of cervical rib on the ground that sensory disturbances were observed "extending 3 or 4 inches above the elbow" (Bramwell and Dykes's case) and "as far up as the axilla" (Thornburn's case) "as if there had been involvement of the second thoracic nerve." He regards these cases as possible examples of rudimentary first rib, but having seen Wrisberg's nerve alone, or reinforced by, or even replaced by the lateral cutaneous branch of the first intercostal, supplying skin down to the elbow, I see no reason for doubting the accuracy of diagnosis in the cases quoted. Rather, this clinical evidence is in favour of the presence of a lateral cutaneous branch from the first intercostal nerve.

GENERAL OBSERVATIONS

Cunningham was the first to observe an intra-thoracic communication across the neck of the second rib between the first and second thoracic anterior rami. He noted its occurrence in 73 per cent. of 37 subjects, Kuntz(15) found it present in 63 per cent. of 48 subjects, Bentley in 58 per cent. of 12 subjects, and I in 65 per cent. of 20 subjects. This intra-thoracic nerve is occasionally directly connected by grey and white rami communicantes with the stellate ganglion, and the bulk of its fibres has, microscopically, the characters of sympathetic fibres. Kuntz has suggested that, when extirpation of the stellate ganglion together with its connected grey rami fails to denervate the blood vessels of the upper limb, section of Cunningham's intra-thoracic nerve should be attempted, to interrupt sympathetic fibres which have entered that nerve either from the stellate ganglion directly or from the sympathetic cord through the second thoracic anterior ramus. Alternately, section of the sympathetic trunk below the level of the second thoracic is advised.

Apart from sympathetic fibres, Cunningham's nerve carries somatic fibres, and its discoverer emphasised the fact that such fibres from D. 2 frequently

pass upwards to join D. 1, and to reach skin of the arm through Wrisberg's nerve, the intercosto-humeral nerve being then smaller than usual. This upward passage of fibres would also account for an intercosto-humeral issuing from the first space, but such a condition I have never encountered.

Since Cunningham ignored any lateral cutaneous branch of N. intercostalis 1, his work requires to be repeated, note being made of the relative

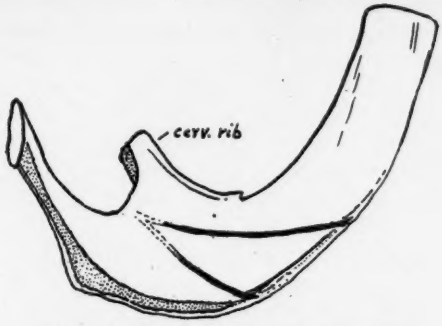

Fig. 3. Showing sulci in case of cervical rib.

Fig. 4. Two modern first ribs showing sulci on inferior surface.

sizes and distribution of all the nerves concerned, the intra-thoracic nerve, the first intercostal, the first lateral cutaneous, the intercosto-humeral and Wrisberg's nerve.

My own impressions are that the size of the nerve of Wrisberg is influenced by that of the first lateral cutaneous, rather than by the size of the intercosto-humeral, and that the relative extent to which the second thoracic nerve supplies the skin of the arm depends largely upon the degree of postfixation of the brachial plexus.

Whilst it is well recognised that the intra-thoracic nerve may contain ascending somatic fibres from D. 2, it is not so well understood that it also contains descending somatic fibres from D. 1, and that such descending sensory fibres may reach their destination (skin along the ventral axial line) either through the second intercostal nerve or through the intercosto-humeral. This may be established by nice dissection, and it explains the presence of sensory twigs to the skin over the first space from the second intercostal nerve—a by no means uncommon occurrence—as also the frequent communications between intercosto-humeral and either Wrisberg's nerve or the first lateral cutaneous. In other words, first thoracic fibres may reach axillary skin by the lesser internal cutaneous, the first lateral thoracic or the intercosto-humeral nerve.

Wilson (*op. cit.*) has figured this downward passage of first thoracic fibres in Cunningham's nerve, in a case wherein the first lateral thoracic nerve assisted in the innervation of the axillary arch muscle.

My best thanks are due to my chief, Prof. J. Kay Jamieson, for much helpful and stimulating criticism; to Prof. J. S. B. Stopford for ready permission to examine material in his Department; to Prof. A. F. Dixon for the kind loan of gorilla ribs; to Mr F. H. Bentley for permitting me to incorporate his findings in this paper; and to Mr P. E. Glynn, prosector, for his valuable assistance in the performance of many tedious dissections.

SUMMARY

1. The course and distribution of the first intercostal nerve is described, a lateral cutaneous branch being noted as constant.

2. Two sulci (*s. diagonalis* and *s. transversus*) on the under surface of the first rib are shown to be produced by the nerve, and may be regarded as a normal feature of the first rib.

3. The corresponding findings in cervical rib and in rudimentary first rib are discussed.

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ADDENDUM

Since writing the above, I have come across a plate by Henle (*Anatomischer Hand-Atlas*, 1874, iv, Angiol. Theil, Taf. CXXXII, Fig. 2, p. 63) of the inferior aspect of the thoracic operculum, wherein the first intercostal nerve and its branches are figured, and are disposed much as I have described. The posterior (deep) muscular twig is double; a collateral muscular branch is shown, but not labelled; and the anterior portion of the main nerve is represented by two branches (neither labelled), one of which may be a lateral cutaneous branch.

No mention is made of these branches in the text, nor do they appear in subsequent plates of the brachial plexus and thoracic nerves.

THE ORIGIN OF THE OS PISIFORME

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The pisiform occupies an anomalous position amongst the bones of the carpus, and in endeavouring to explain its presence various theories have been formulated. Flower and Mivart placed it with the sesamoids; Bardeleben considered it to be a skeletal vestige of the post-minimus; while others again treat it as a true carpal element. This paper supports the latter view, and is primarily an attempt to reconcile the bone with the primitive structure of the carpus.

THE SESAMOID THEORY

With reference to the Sesamoid Theory it must be admitted that the human pisiform is superficially suggestive of a sesamoid in size, shape and in its relation to the tendon of the M. Flexor Carpi Ulnaris, as a typical sesamoid is a small bone situated in a tendon; but in the extinct marsupial *Diprotodon australis* Owen, the pisiform is the largest member of the carpal series and comparable to the calcaneus. Again, sesamoids are not characterised by their articulations with other bones, whereas the pisiform typically contributes to the formation of a joint, such as the Articulatio Ossis Pisiformis of the human carpus. The position of the joint is not constant, for while the primitive site of the pisiform is in the vicinity of the articulation between the ulna and ulnare (or cuneiform) on its lateral aspect, the bone may occupy various positions along the post-axial margin from this situation to the fifth metacarpal; in man it articulates with the cuneiform; in *Hyrax*, with the cuneiform and unciform; in *Chelone imbricata*, the unciform; and with the fifth metacarpal in certain Chelonia.

One of the best instances of a massive joint in which the pisiform plays a prominent part is in *Diprotodon australis*, where the cuneiform and pisiform both articulate with the ulna by means of a hemispherical socket formed by the two bones, thus forming a typical Enarthrosis.

In another respect the pisiform differs from a sesamoid, in occasionally fusing with certain of the neighbouring bones, as in certain of the Chelonia, where the pisiform may coalesce with the third, fourth and fifth carpals. This tendency to fusion is not unusual in regard to the other carpal bones as exemplified by the scapho-lunar of the Carnivora, and the consolidation of the fourth and fifth distal carpals in the formation of the mammalian unciform.

THE PISIFORM AS A VESTIGIAL POST-MINIMUS

This theory obviously supposes a Polydactylous manus, and while admitting that Polydactylism probably antedated Pentadactylism, the evidence so far advanced in its support appears to be inconclusive and insufficient to establish it as a fact. Many of the instances cited can be reconciled without undue difficulty with variants of the pentadactyl limb, as was done by Howes and Hill with regard to the so-called pre-hallux of the Dorking Fowl, which was shown to be due to fission of the hallux.

Again the fundamental inertia of nature towards the creation of new types is axiomatic, and appears in vivid contrast to the prodigality of variety in existing ones.

It is suggested that the most convincing evidence of Polydactylism will eventually be found in fossil forms, but in ones much more primitive than those at present known.

THE PISIFORM A MEMBER OF THE CENTRAL SERIES

The primitive pentadactyl manus as conceived by Gegenbaur with its carpus of three proximal elements, two centralia and five distalia has been of great value in the past. But since then, it has been shown that a few animals possess three centralia as in *Broomia*, certain Theromorphs, and the embryo of *Sphenodon*.

Broomia, described by Watson from South Africa, is a fossil reptile which differs from all other pentadactyl vertebrates in having the five distalia, and four proximal carpalia, completely separated from one another by the three centralia, thus it will be seen that the carpus of this animal is composed of three distinct rows of bones. Hence it would appear that *Broomia* introduces a more primitive type of carpus than any previously known, consequently the primitive pentadactyl manus of Gegenbaur must be modified with regard to the central series. In passing it should be noted that the carpus of one of the earliest known tetrapods, the Stegocephalean *Eryops*, does not present features so primitive as *Broomia*.

So far little has transpired to necessitate changes in Gegenbaur's conception of the remaining bones of the carpus, i.e. those forming the proximal radiale, intermedium, and ulnare on one hand, and the five distalia on the other. On considering the pisiform, however, it does not appear to belong to the proximal series, and with much less reason to the distalia; therefore either its affinities are with the centralia, or it represents a distinct element in the carpus.

The centralia during the course of evolution have undergone senescence, and this has resulted in the gradual approximation of the proximal and distal series; a movement which began on the ulnar side of the carpus. In the remaining forms with three centralia the most radial is exposed on the pre-

axial border like that occurring in *Broomia*, and is to be regarded as a primitive feature[1]; but such a series, however, considered as a whole, is degenerate to that of *Broomia*. The next stage in degeneration is a reduction to two centralia accompanied by a radial approximation of the proximal and distal series which now surround the bones. Following this the centralia are reduced to a single representative, the most common condition, and finally there is fusion with the scaphoid or complete disappearance altogether. In man the centrale fuses with the scaphoid, but occasionally may remain discrete as a variation. The mammalian centrale is regarded by Williston as the second member of the centralia.

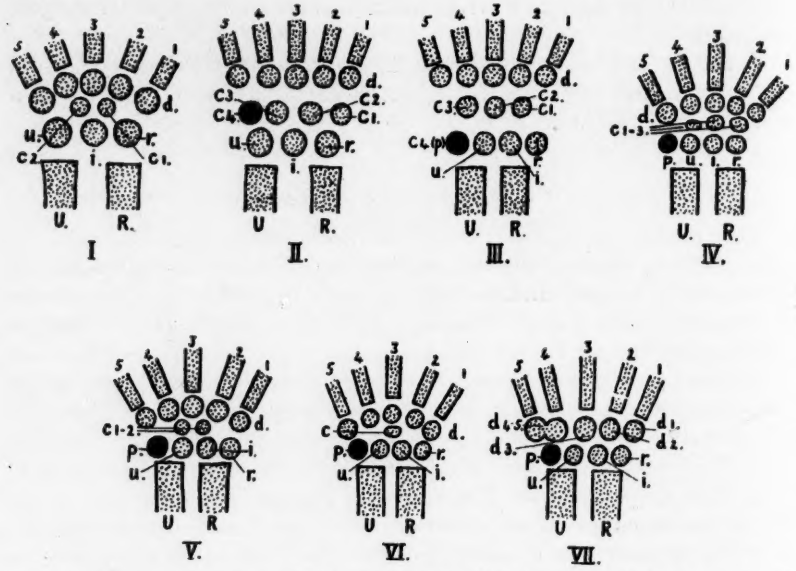

Fig. 1. Diagrammatic carpal types illustrating the origin of the pisiform and the degeneration of the centralia. I. Gegenbaur's primitive carpus. II. Suggested primitive carpus. III. *Broomia* with the pisiform homologised with the fourth central. IV. *Sphenodon* (embryonic). V. *Sphenodon* (adult). VI. *Lacerta*. VII. Human. 1, 2, 3, 4, 5, metacarpals; *C* 1, *C* 2, *C* 3, *C* 4, centralia; *C* 4 (*p*) transposed 4th central or pisiform in III; *d*, *d* 1, *d* 2, *d* 3, distalia; *d* 4–5, fused 4th and 5th distalia in VII forming unciform; *p*, pisiform indicated in black; *i*, intermedium; *R*, radius; *r*, radiale; *U*, ulna; *u*, ulnare.

The position of the pisiform in *Broomia* is suggestive, and as the bone is a well-known wanderer, it requires very little alteration of position to put it in with the centralia. It is suggested that the pisiform is a fourth central, and that its movement toward the proximal carpalia was the first stage in the senescence of the central series.

[1] Occasionally in forms with one or two centralia, the pre-axial margin is reached, as in Macacus.

The necessary alterations in the carpus of the primitive pentadactyl manus are given in fig. 1, II. It will be seen that following the radius and ulna are the three proximal carpalia (radiale, intermedium and ulnare) which are completely separated from the five distalia by four centralia. This carpus is practically that of *Broomia* with the pisiform transposed to the centralia.

It is interesting to note that an arithmetical series is formed by the number of bones on proceeding from the humerus to the distalia, viz.:

(1) Humerus	... ...	1 bone
(2) Radius and Ulna	... ...	2 bones
(3) Proximal carpalia	... ...	3 ,,
(4) Centralia	... ...	4 ,,
(5) Distalia	... ...	5 ,,

SUMMARY

(1) The primitive carpus consisted of twelve components arranged in three rows.

(2) There were three proximal and five distal carpalia, completely separated from one another by an intermediate series of four centralia.

(3) The most ulnar of the centralia was displaced to the lateral margin of the ulnare and became the Pisiform.

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A CASE OF CRANIOPAGUS PARIETALIS

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CLINICAL HISTORY

The female double-monster to be described was born on 10 December, 1927, of a healthy primiparous woman. The larger individual (subsequently referred to as *A*) was delivered first by the breech, the smaller (*B*) following without any marked delay.

It was then apparent that the two individuals were united head to head, facing in the same direction, with their axes inclined at an angle of about 15° to one another. There was also a slight degree of rotation of the axis of one on that of the other. There were two independent umbilical cords, but a single placenta.

From birth *A*, the larger, flourished and took the breast well as compared with *B*. The combined weight at birth was 8 lb. 4 oz., of which (from post-mortem data) 5 lb. belonged to *A*, and 3 lb. 4 oz. to *B*.

The monster was admitted to Guy's Hospital on the fourth day of life. It was then clear on clinical examination that the union of the two individuals was superficial only. *A* was frequently placid or sleeping, while *B* was fretful and crying. Stimuli (e.g. pin pricks) applied to one produced no response in the other. The pulse, respiration and temperature of the two showed slight differences. Blood counts were identical, and indigocarmine injections showed that there was some slight connection between the two circulations.

As it appeared that *B* was not likely long to survive, an attempt was made on the twelfth day of life to separate the two by operation. It was realised that the smaller of the two must be sacrificed, and a skinflap was accordingly marked out on *B* in the occipito-parietal region to be used in closing the defect on *A*. Anaesthesia was induced in *B* without any effect on *A*. The flap was reflected and the right parietal bone of *B* divided some distance from the line of union. The dura was then separated from the bone until this line was reached. Further separation of the dura of *B* from either the bone, or the dura of *A* was found to be impossible. The dura was then incised. This resulted in the sudden escape of a considerable quantity of cerebro-spinal fluid, and the simultaneous death of both individuals.

POST-MORTEM FINDINGS

Death having taken place on the operating table, a coroner's investigation was necessary.

At the autopsy, the separation begun at operation was completed. It then became apparent that the dura was deficient between the two brains

over a large area on the side towards which the axes inclined. An oval opening, 2 inches wide, was found, outlined by a slight ridge on the inner surface of the skulls at their junction, and a falciform fold of dura in the coronal plane near the mid-line. Unfortunately no note was made of the state of the arachnoid in this situation, but the two hemispheres were in close contact and flattened one against the other.

Between the other two hemispheres a fold of dura passed from the line of union peripherally, towards the middle line. The falx cerebri of each child was attached to this, and it ended just beyond the middle line in the free falciform edge already mentioned.

There was no bony union between the two, but the parietal and frontal bones of each had a straight upper border connected by fibrous tissue across the line of union. In front, there was a diamond-shaped fontanelle between the four frontal bones. At the back, each had a separate posterior fontanelle, and between these there was an irregular deficiency in the skulls between the left parietal bone of *A*, and the parietal bones of *B*.

Apart from a slight degree of asymmetry, the brains of the two were normal. Nothing markedly abnormal was noted in the rest of the bodies. Both pairs of kidneys showed foetal lobulation. The caecum of *A* was infantile in type, while *B*'s was normal. The right ovary of *A* was cystic, while a single cyst was present in the right ovary of *B*.

Both individuals showed such a marked degree of development of the clitoris, that this organ on superficial examination might have been mistaken for a penis. The external and internal genitalia were however of the female type, and there was no true hermaphroditism.

Ossification had commenced in all four lower femoral epiphyses.

FURTHER INVESTIGATION

After post-mortem examination, the bodies were further dissected in order to determine whether any slight variations present in one were reproduced in the other, and if so, whether the twins were identical or mirror images.

The only additional point noted at the line of union was the presence of a small venous sinus passing from one superior longitudinal sinus to the other, along the irregular line of union already mentioned at the back of the skulls.

Dissection showed the following points worthy of note:

(1) All four lower limbs showed the presence of an accessory obturator nerve (from L. 3 and 4) which passed to the adductor muscles over the pelvic brim. They were, however, too small to trace to their distribution. Normal obturator nerves were also present in all four lower limbs.

(2) All four palmar arches showed the same variation, namely, a large median artery passing into the palm to join with the ulnar. The radial arteries were very small and took hardly any part in the formation of the arches.

On the right side of each, the radial artery was very small and had no superficial volar branch. On the left side of each, a very small superficial branch was present. The median artery in each palm supplied digital branches to the index finger and radial side of the middle finger. The ulnar artery in each hand supplied the remaining fingers on the ulnar side.

(3) In the left forearm of *B* the palmaris longus was abnormal. The muscular belly was situated half-way down the forearm and was fusiform in shape, being connected by a long flat tendon to the rest of the flexor muscles arising from the internal condyle. In the other three forearms a normal palmaris longus was found.

DISCUSSION

All degrees of fusion of two individuals have been met with and described, both in man and in animals, and the relative size of the two component parts may vary between wide extremes. At one end of the scale are found the monsters composed of two equal-sized and fully developed individuals (as in the present case). At the other end, are the parasitic forms where a relatively small and shapeless foetal mass is attached to some part of a more fully developed individual. The sex of the two parts is, of course, always the same, but all types of double monsters are more commonly female than male in the proportion of 3/1 (approx.). In craniopagous types the preponderance of females is even greater.

Fusion can occur in one of three planes. The commonest form is where the two individuals may be considered as lying side by side, and joined down one side. The usual result is some form of dicephalic monster, or else a monster with single head and double body. Many variations of this type are known.

The next most common form is where the two individuals are opposed to one another by either their ventral or their dorsal surfaces. In the former case

fusion results in either a thoracopagous (supra-umbilical) or iliopagous (sub-umbilical) monster. Dorsal union results in the various types of pygopagi.

The rarest type of double monster is that in which the axes of the two individuals are placed end to end. It is to this group that cases of craniopagus parietalis belong. The union may, however, be at the caudal end, resulting in an ischiopagus.

The total number of recorded cases is not large, but the following table collected by Tartuffi (see Marchand (1)) shows the relative frequency of each.

Cases collected by Tartuffi.

Thoracopagi	86
Pygopagi	22
Ischiopagi	7
Craniopagi	2

Schwalbe (2) describes three types of craniopagi, viz. frontal, occipital and parietal. He points out, however, that the first of these is in reality an extreme variety of thoracopagus (i.e. union by the ventral surface), while the second, or occipital type, belongs to the pygopagi. It is only in the parietal variety that the axes of the two individuals meet end to end.

Schwalbe had met with no case of craniopagus parietalis in his own experience, but quotes one or two from the literature on the subject. Thus Von Baer (3) described a female craniopagus born in Bruges in 1682. A case described in some detail by Otto (4) shows such a striking resemblance to the present one that it may be mentioned more fully. The monster was born at the fifth month and consisted of two female individuals joined by their vertices. Their axes were described as slightly twisted on one another. A small furrow in the skin showed the line of separation of the two individuals. Dissection showed that there was some vascular, but no nervous continuity across this line. The bones of the vertex were wanting, and the underlying dura mater was also deficient over one hemisphere. On the opposite side, a single layer of dura separated the two brains. On the side where the dura was deficient, the hemispheres were flattened against one another, but there was a distinct arachnoid membrane and a separate sub-arachnoid space to each individual.

The case here described agrees very closely with Otto's. It is clear that in this type of monster the brains are separate but in very close contact over one or both hemispheres, with a deficiency of the dura mater between them.

Attempts to separate the two individuals are therefore unlikely to succeed owing to shortage of dura mater to cover the defect.

In considering the mode of formation of double monsters, the view commonly held is that they result from the splitting at any early stage of a single embryonic disc along the line of the primitive streak. If the separation of the two halves be incomplete at the cephalic end, a craniopagus monster results.

The axes of the two individuals may later become twisted so that they come to lie more nearly end to end. There will however be some angulation left. This, according to Schwalbe(2), is the mode of formation of the frontal and occipital craniopagi.

The fact that in both the present case and in Otto's case a slight angle was present between the two axes, suggests that craniopagus parietalis is only a further stage in the same process. This would also account for the deficiency of the dura mater over one hemisphere and its presence over the other.

If the two individuals developed originally side by side they should be mirror images. Unfortunately of the three variations from normal noted above, two were bilateral, and the third was present in one individual only.

Another possible explanation of the formation of these monsters is that they developed from two separate primitive streaks lying end to end. In such a case the separation of the two individuals would date from a much earlier period in their development, and variations in the one would be less likely to occur in the other. On such a hypothesis, however, the further development of two individuals, joined by the head, so as to lie within a single amnion is difficult to explain.

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REVIEWS

The Cytoarchitectonics of the Human Cerebral Cortex. By CONSTANTIN VON ECONOMO, Professor of Neurology and Psychiatry in the University of Vienna. Translated by Dr S. PARKER. (Oxford University Press.) 1929. Pp. 186. Figs. 61. Price 21*s.* net.

Professor von Economo's great work, *Die Cytoarchitektonik der Hirnrinde des erwachsenen Menschen*, was published in 1925 and reviewed in this *Journal* (vol. LXI (1926–7), p. 264). The present work, translated into English by Dr S. Parker, is a condensation—an abstract of the essentials—of his great book and atlas. The author has also taken the opportunity to introduce modifications and additions which are new. For English anatomists and medical men generally, the present work will be a boon, for it presents them with an excellent summary of the present state of knowledge concerning the microscopic structure of the cortical areas of the brain. A comparison between the final cortical maps now published and those which Professor Elliot Smith contributed to this *Journal* in 1907, demonstrates a close correspondence and shows how reliable are the naked-eye methods which were used by Professor Elliot Smith. Chapters I and II are devoted to the lamination of the cortex, the constituent elements of each layer, the various grades of cortex, and a description of the methods which the author has employed in his investigations. A new system of dividing the brain into lobes is described, the lobes corresponding, not to gross markings, but to the type of structure revealed by a microscopic examination of the cortex. Chapters III and IV are given to the frontal lobe, chapters V and VI to the parietal lobe, chapter VII to the insular lobe, chapter VIII to the occipital lobe, chapter IX to the temporal lobe, and chapters X, XI to what was formerly named the "limbic" lobe. The final chapter, the most interesting of all, is devoted to the manifestations of the living cortex, consciousness being regarded as "the specific sensory energy of the cerebrum." Finally, the "natural law of progressive cerebration" is discussed.

Brain and Mind or the Nervous System of Man. By R. J. A. BERRY, M.D., Dean of the Faculty of Medicine and Professor of Anatomy in the University of Melbourne. (Macmillan Company, New York.) 1928. Pp. 608. Figs. 130. Price 31*s.* 6*d.* net.

In the previous issue of this *Journal* there was reviewed Professor Wood Jones' *Matrix of the Mind*, a book which gives a lucid and original account of the central nervous system as seen from a personal point of view. Professor Berry's book is more systematic, more ambitious, although not less personal, for all through its forty-three chapters the author's individuality and predilections are palpable. The aim of the book is to describe the central nervous

system as a physiological structure having an anatomical basis—the only profitable way of approaching the most complex system of the human body. In the first chapter the author leaves his readers in no doubt as to his conception of *mind*: "the neuron is the physical instrument of mind," he writes; "consciousness, memory, speech, thought and reason can manifest themselves only when there is a sufficiency of neurons for the purpose" is another of his introductory statements—all of which he proceeds to substantiate in chapter after chapter.

Having established the reflex arc as the unit out of which the central nervous system has been elaborated, the author makes his approach through the spinal cord and works step by step until the cortex of the brain is reached. He calls to his aid the latest teachings of evolution, of embryology, of anatomy, of histology, of physiology, of pathology and of medicine, to help him in his task of description. He makes his text the more easily understood by a free use of diagrams, although it must be confessed that many of these are more effective than artistic.

It is not possible in the bounds of a brief notice such as this to enter into the detailed exposition given by the author; a book which covers and combines so many departments of knowledge, all of them expanding daily, could not but be open to the criticism of specialists, but even if we allow such criticisms as valid, nevertheless this work is the best introduction to a knowledge of Man's nervous system that has yet appeared in the English tongue.

Professor Berry sees in the cortex of the brain the instrument of human intelligence and hence devotes to it a very large part of his book. He rightly introduces his own work on the growth of the brain in childhood; the measurements made by him and Dr Porteous provide the most reliable data we possess concerning the times and the individual variations in the growth of the human brain. We are glad to note that he gives a full account of the pioneer work which Dr Joseph Bolton did on the cortex of the brain during the earlier years of the present century.

Contributions from the Department of Anatomy of the Peking Union Medical College, Peking. Vol. IV. Collected Papers. Nos. 58–83. 1927.

Although the notice of this important volume of papers is belated the fault cannot altogether be laid to the editors; so varied are its subjects of research that it has taken sometime to find a reviewer with qualifications equal to the scope of the volume. Altogether 26 papers are included; 7 of these deal with histological or embryological problems; 3 are devoted to human anatomy; 8 are anthropological; 4 deal with comparative anatomy; 2 with prehistoric man; 2 are historical. It says much for the enthusiasm which the Director of the Anatomical Department of Peking Medical College has succeeded in instilling into his staff and his pupils that such a varied and valuable series of researches could make its appearance. Less than half of these researches have

been published in Journals and Proceedings which are accessible to anatomists of America and Europe. Some of them have appeared in the *American Journal of Anatomy, Anatomical Record* and the *Proceedings of the Academy of Science of Amsterdam*; others, unfortunately, will be available only to such schools as may have the fortune to possess this volume or the remote publications in which they first appeared.

The following papers by Professor Davidson Black are included. (1) An important survey of evidence relating to the distribution of primate forms in the past and present; the facts of distribution, he holds, can be explained only if we suppose that Central Asia has throughout been a cradle of evolution and a centre of distribution. (2) A preliminary description of human remains from various parts of China representing the people of the eneolithic period; a type occurs with Europeanoid features. (3) The announcement of the first discovery of remains of early pleistocene man at Chou Kou Tien. (4) An outline of the course given in his laboratory on the anatomy of the central nervous system, from which it is apparent that medical students are given such a course in neurological anatomy as is nowhere to be obtained in England.

Dr P. H. Stevenson contributes 8 papers on anthropological subjects—most of them relating to the growth and anthropometry of the Chinese. Two of these deserve particular mention—his instructions to travellers who wish to make records of physical measurement of the living peoples; and his method of calculating the body-surface of Chinese.

In his choice of subjects for investigation, Dr A. B. D. Fortuyn manifests an even greater range of choice than his chief. Nuclear division, embryology, teratology, neurology, neuropathology, comparative anatomy, natural history and heredity are amongst the subjects of his investigations. Particularly valuable is his descriptive account of 400 specimens contained in the embryological collection which is being assembled in the Medical College at Peking. Almost the entire collection represents normal or abnormal embryos or foetuses of Chinese parentage. Racial marks appear early. Dr Stevenson's pamphlet on the laws of variation and heredity is well worthy of study. Besides these papers are others of value by Chinese students, evidence that the Western Science of Medicine is being successfully established in the capital city of China.

A Synopsis of Regional Anatomy. By T. B. Johnston, M.B., Ch.B., Prof. of Anatomy, University of London, Guy's Hospital Medical School. 2nd edition. (London; J. & A. Churchill.) 1928. Pp. 456. 11 Text-figs. Price 12*s.* 6*d.*

This book is intended, the author states, "to assist the average student in the revision of his anatomy, after his dissections have been completed." If the student then feels in need of a book other than his accustomed practical manual, this one can be recommended as likely to succeed in achieving its

professed purpose. It provides a clear and concise account of regional anatomy without resort to the three distressing devices commonly adopted to secure conciseness—syncopated text, abundance of small type and meaningless tables of relations. The necessity for studying dissected "parts" as the book is being read is repeatedly insisted on, and there are no illustrations to distract the student's attention from actual dissections. The only figures are line drawings accompanying a useful statement of the internal structure of the spinal cord and brain stem. The account given of structures and relations seems reasonably full. Some minute branches of arteries and nerves which, as the author says in one instance, "have gained a totally undeserved notoriety," are wisely ignored. The only definite structures whose absence really obtrudes upon one's consciousness are the palmaris brevis and the deep head of the flexor pollicis brevis. The lymph drainage of the tongue perhaps requires fuller treatment. It is hardly correct to locate the atrio-ventricular node "in the lower and anterior part of the inter-atrial septum." But these are solitary points noted for critical comment in a book whose lucid style secured for itself a fairly complete perusal.

Researches in Craniometry. By JOHN CAMERON, M.D., Professor of Anatomy, Dalhousie University, Halifax, N.S. 1928.

The University of Dalhousie has been well advised to issue this volume; it contains a consecutive series of exact studies made on the skull by Professor John Cameron. At the end of the volume is printed a most welcome list of Professor Cameron's various researches—from 1901 to 1928. The list begins with a study "On the Movements of the Processes of Retinal Pigment Cells," published in 1901. Up to 1918 Professor Cameron's papers deal chiefly with histological and embryological subjects; but in that year he began to be interested in the problems of the human skull and for the last decade has given himself to craniology. In the present volume only two papers belong to his earlier period; one deals with the histogenesis of striated muscles, the other with a neurotropic phenomenon manifested by the neuroblasts of the ganglionic layer of the retina. These appeared originally in the *Transactions of the Royal Society of Canada* (1917, 1921). All the other studies included in this volume —23 in number—are craniological or anthropological. All have been carried out since 1924, and have appeared in the *Transactions of the Royal Society of Canada* or the *American Journal of Physical Anthropology*—except a *Report on the Osteology of the Central and Western Eskimo*, which was issued by the Government of Canada. The value of Professor Cameron's researches is enhanced because of the material on which they are based. With great liberality Professor Wingate Todd of Western Reserve University, Cleveland, Ohio, placed at his colleague's disposal the justly famed collection of skulls and skeletons which he has assembled in the Hamann Museum of his University. It is the only collection in the world where sex, age and race of each skull

and skeleton are beyond dispute. Professor Cameron's studies are based on the Hamann collection; he had at his disposal the skulls of 409 white Americans (358 males, 51 females); 190 Negroes (153 males, 37 females); these were sectioned skulls and thus all basal parts were available for exact measurement. The studies begin with the elaboration of a method for measuring and registering the flexion or bending of the basal axis of the skull—the variations met with according to individual, age, sex and race being measured and registered. Professor Cameron criticises, somewhat unfairly we think, the classical investigations made by Huxley on the bending of the basi-cranial axis, but he is undoubtedly right in regarding the pituitary region of the base as the chief site of flexion as far as the skull of the higher primates is concerned, and the method which he has employed is one which will prove acceptable to all craniologists. All the same, the ethmoidal segment of the base does, as Huxley demonstrated, undergo bendings and unbendings independently of those which occur at the pituitary hinge of the base.

As has been said, Professor Cameron's investigations follow consecutively, one after another; passing along the base of the skull from basion to nasion, he analyses its various constituent parts—their dimensions and their angles. Reaching the nasion, he then begins an analysis of the frontal arch of the skull, inventing new and better ways of registering its curvature, its slope and its relation to the prepituitary part of the base. He finds that the prepituitary base is longer, absolutely and relatively, in the skulls of whites and correlates this with the greater brain of the white man, as contrasted with the shorter prepituitary region of the negro. The correlation of the diameters of the skull to cranial capacity is worked out for a number of racial groups. Several studies are made of Eskimo and Mongol collections of skulls.

The volume is one which ought to be consulted by all craniologists—for its methods as well as for its facts and results. Professor Cameron has gracefully acknowledged his indebtedness to the Hamann Museum by dedicating this volume of his researches to Professor and Mrs T. Wingate Todd.

Handbuch der Anatomie des Kindes. By Drs Peter, Wetzel and Heiderich. Erster Band, I. Lieferung. (Munich; Bergmann.) 1928. Pp. 189. Figs. 73. Price 29·5 marks.

The first part of the second volume of this valuable handbook was published last year and the first part of the first volume has been awaited with interest. This part deals essentially with the connective tissue, the specialised derivatives thereof such as cartilage, bone and muscle, the blood, the blood-forming organs, the marrow, the lymphatic glands and the spleen. The book is of great service to workers in all fields of medicine as the physiological and pathological outlooks are so well maintained.

The gross and minute anatomy of the tissues, the range of form and of size in the various cells, and their changes with age are dealt with in detail,

Wetzel has succeeded in sorting out the mass of material relating to the blood count of babes and has presented the prevailing views with the aid of an exhaustive series of tables and graphs. The account of the haemopoietic system is a model of thoroughness, and the data range from the still-born to adolescence. Haemoglobin percentage, colour index, Arneth differential count and blood platelets are surveyed up to date, and the description of the spleen includes the recent work of Barcroft and his co-workers. The book is earnestly commended to workers who are seeking for statistical data as no text book of Anatomy or Physiology provides such a mine of information.

A Short Course on Human Osteology. M. R. Drennan, M.A., M.B., Ch.B., etc., Professor of Anatomy in the University of Cape Town. The Mercantile Press, Cape Town. 1928. *7s. 6d.*

Perhaps the most striking feature of Professor Drennan's *Short Course on Human Osteology* is the complete absence of figures. That this may be a drawback Professor Drennan confesses in the Preface. However, the absence of figures may, as far as the student is concerned, be a blessing in disguise. The bones themselves certainly furnish the best illustrations and if the student will consent to study the actual bone with Professor Drennan's description for his guide no better method of attaining familiarity with the human skeleton could be devised.

The radial sulcus on the humerus is a wide groove and the fact that it serves for the attachment of part of the brachialis muscle in addition to affording accommodation for the radial nerve and profunda brachii vessels receives no mention. The accentuation of the pre-auricular sulcus is given as a distinguishing feature of the female pelvis but what the pre-auricular sulcus is and where it is to be found are left to the imagination of the reader. That the sacrum is less curved in the female than in the male is a statement open to criticism. The greater uniformity in the curvature of the male sacrum as compared with that of the female, which is flatter in its upper part and more curved in its lower, are more valuable diagnostic features. The description of the pterygoid processes of the sphenoid and their laminae is far from clear and which of the two is concerned in bounding the pterygoid notch and the pterygoid fossa is open to considerable doubt.

However, no descriptions of the skeleton or of any part of the human body are above criticism. Professor Drennan's treatise has the great merits of being concise, well designed and free from superfluous detail. If used as it is intended to be used it should prove an invaluable aid to the student. A pleasing addition to the book, which is of very handy size, is the presence of blank interleaves which will prove of great service for additional notes or for drawings made by the student himself. The absence of an index is a surprising omission which we hope will be remedied in a subsequent edition.

Histologischer Atlas von Zupfpräparaten unfixierter menschlicher Organe und Gewebe. By Dr Hanns Plenk. Julius Springer, Vienna, 1928. 6 Reichsmark.

There is a tendency in a branch of Science such as Histology, with its wealth of new methods, to discard the older techniques in favour of the newer ones, irrespective of their relative values. This book by Dr Hanns Plenk draws attention to one of the oldest methods of histological study, the microscopic examination of teased organs and tissues, and throws new light on its possibilities as a means of training students in accuracy of observation. The scheme of the book is based upon the course of instruction given to students in Vienna University. It assumes that the student is already acquainted with the general outlines of the histology of the tissues and organs. In the introduction the author expresses the hope that the book may not only be of use to students, but may be welcome to professional workers, and especially to those engaged in tissue culture who need to be able to recognise isolated unfixed tissue elements.

The descriptive part of the book is divided into three sections. The first part gives a brief account of the best method of preparing teased preparations. This is followed by a section devoted to the description of "things present in most teased preparations," which includes fat droplets, air bubbles, impurities, and the cells of the blood and connective tissue. The third, and largest section, describes selected organs and tissues as they appear in teased preparations. Twenty-eight plates, comprising forty-seven figures, are given in illustration. Most preparations are figured at two magnifications—a hundred and thirty, and four hundred and fifty times the original. They should enable the careful observer to identify readily the cellular elements of the tissues they portray.

In a future edition the author might be prevailed upon to increase the scope and usefulness of his work by introducing the use of some supra-vital staining methods, such as neutral-red and Janus green, which are quite within the technical abilities of the elementary student. The difficulty such methods involve of requiring perfectly fresh material—and Dr Plenk is dealing primarily with human organs and tissues—has no doubt been foreseen by him. The book as it stands, however, well fills the place it is intended to occupy in histological literature.

An Introduction to the Study of Experimental Medicine. By Claude Bernard. Translated by Henry Copley Greene, A.M. With an Introduction by Lawrence J. Henderson, Professor of Biological Chemistry, Harvard University. (New York: Macmillan Company.) 1927. 6″ × 9″. Pp. 19 + 226. Distributed by the courtesy of the Rockefeller Medical Foundation, New York.

Anyone desirous of regaining that sense of proportion which is all too rare in this day of specialisation, with catch phrases as a means of enforcing premature conclusions, and an expression of one's own state of mind as a substitute for reality, should read this *Introduction to the Study of Experimental Medicine* by Claude Bernard. The avalanche of medical publications since

his time indicate that heightened activity is not necessarily synonymous with true vision.

This succinct justification of the true Anatomy must be quoted *in extenso:*

> Anatomy is the necessary foundation of physiology, and never can we become good physiologists if we are not first deeply versed in anatomical studies and trained in delicate dissections, so as to be able to make the preparations which are often required for physiological experiments. In fact, operative anatomical physiology has not yet been founded; the zoologist's comparative anatomy is too vaguely superficial for physiologists to find in it the exact topographical knowledge that they need; the anatomy of domestic animals is done by veterinarians from too special and restricted a point of view to be of great use to experimenters, and thus physiologists are ordinarily reduced to making for themselves the anatomical investigations which they need to devise their experiments. It is evident that, in severing a nerve, tying a duct or injecting a vessel, knowledge of the anatomical arrangement of parts, in the animal operated on, is absolutely indispensable to understanding and defining the physiological results of the experiment. Some experiments would be impossible with certain species of animals, and intelligent choice of an animal offering a happy anatomical arrangement is often a condition essential to the success of an experiment and to the solution of an important physiological problem. Anatomical arrangements may sometimes present anomalies which must also be thoroughly known, as well as the variations observed between one animal and another. In the sequel of this work, I shall therefore be careful always to describe experimental methods, including the anatomical arrangements, and I shall show that divergencies of opinion among physiologists have been caused, more than once, by anatomical differences which they failed to reckon with, when interpreting the results of experiments. As life is merely a mechanism, anatomical arrangements peculiar to certain animals may seem insignificant at first sight; yet these seemingly futile minutiae are often enough to change the physiological manifestations completely and to form what we call a highly important idiosyncrasy. A case in point is section of the two facial nerves, which is mortal in horses, but not mortal in other closely related animals.

Three Lectures on Neurobiotaxis and other subjects delivered to the University of Copenhagen. By C. U. Ariëns Kappers. (Heinemann, London.) 1928. Pp. 76. Figs. 11. Price 7*s.* 6*d.* net.

Dr Ariëns Kappers has done his colleagues a service by publishing the three lectures he gave to the University of Copenhagen in 1927. They deal with problems to which he has contributed more than any other anatomist. In the first lecture he gives many new instances, some observed by himself, others by younger workers, to illustrate the wide application of the law of Neurobiotaxis to an explanation of the evolution of all parts of the brain—particularly of the cortex. In the second lecture he expounds his present conception of the corpus striatum—both as regards its evolution and its function. The third lecture is devoted to the evolution of the cortex of the brain, particular consideration being given to the steps which led up to the differentiation of the supragranular layers of the cortex. While we think the price is high considering the size of the pamphlet, yet we admit that it makes up in quality for what it lacks in quantity.

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THE HISTOLOGY OF AN HERMAPHRODITE PIG AND ITS DEVELOPMENTAL SIGNIFICANCE

By F. W. ROGERS BRAMBELL
Lecturer in Zoology, King's College, London

(*From the Department of Anatomy (Histology and Embryology), University College and the Department of Zoology, King's College, London*)

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I. INTRODUCTION

The example described in this paper is essentially similar to many of the pigs exhibiting hermaphroditismus verus lateralis described by Pick (9) and other authors, and more recently by Baker (1, 3) in this country. The gross anatomy presents no points of importance which have not been recorded by these authors and therefore only requires brief description. The histology of the ovotestes of such pigs has not received, however, adequate attention although it merits accurate description. This aspect, in the present instance, is of prime importance, since it reveals several facts of considerable interest and of theoretical significance, such as the presence of a cortical zone of spermatic tissue outside the tunica albuginea, the tubules in which open on the peritoneal surface by pores, and the occurrence of true oocytes in spermatic tubules.

The author is indebted to Mr A. S. Foster through whom the material was obtained, and to Prof. J. P. Hill, F.R.S., and Mr J. R. Baker for valuable criticism and advice. The histological expenses were defrayed from a grant from the Government Grants Committee of the Royal Society for which the author's thanks are due.

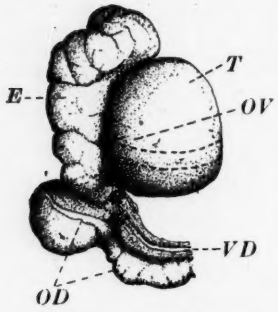
II. DESCRIPTION

General description

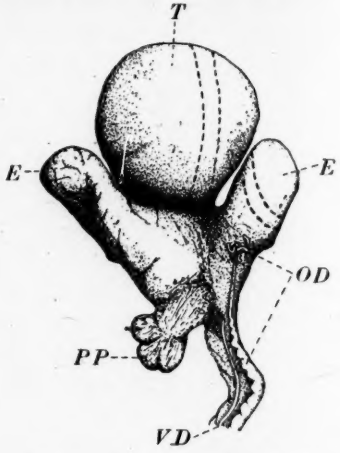
The material described was removed from a young pig, about six weeks old, as gonadectomy is customary with animals intended for bacon. The gonads and associated structures were then dropped intact into a bottle of Bouin's fluid

in which they remained until they were received by the author some days later. It is understood that the external genitalia of the pig in question were abnormal in character, and that similar cases have occurred before on the same farm. Unfortunately no other information, apart from that derived from the fixed material, is available.

The material consists of the two gonads and epididymides, the two uterine cornua and part of the median portion of the uterus and two vasa deferentia. The right gonad, which was the smaller, proved to be an ovotestis. It measured about 17 mm. in diameter and was rounded almost spherical in shape (text-fig. 1). The left gonad was a testis and measured 22 mm. in diameter (text-fig. 2). Both gonads presented a firm smooth surface like that of a normal testis and



Text-fig. 1. Right gonad, showing ovarian patch on testis. *T*, testis. *OV*, ovary. *E*, epididymis. *OD*, oviduct. *VD*, vas deferens. The double dotted line across the gonad indicates the plane of section. × 1·2.



Text-fig. 2. Left gonad showing the convoluted tip of the oviduct and the pampiniform plexus, *PP*. Other letters as in text-fig. 1. × 1·2.

each was attached by a broad hilum (Plate I, figs. 1 and 2). The epididymides were large, convoluted and roughly L-shaped, that on the left being somewhat larger than the right. The hilum of the testis was attached to the longer arm of the L in the angle of each epididymis. A pampiniform plexus was present on each side attached to the epididymis (Plate I, figs. 1 and 2). Sections showed that the tubules of the epididymides were empty and devoid of spermatozoa (Plate I, fig. 3).

The uterine cornua and vasa deferentia were attached to the outer sides of the angles of the epididymides (text-figs. 1 and 2). The uterine cornua were much convoluted and measured approximately 3 to 3·5 mm. in diameter throughout the greater part of their length. They tapered to a point on the surfaces of the epididymides, to which their extremities were closely attached, and

the extremity of that on the left was convoluted (text-fig. 2), while that on the right was straight. The median uterus, close to the point where the two cornua fused, measured 3·5 mm. in diameter. The uteri, though small, were well developed and the mucosa was thick and full of glands (Plate I, fig. 4). The vasa deferentia, after leaving the epididymides, extended back on each side, parallel to the cornua in the uterine mesentery. They were applied to the ventral wall of the median uterus on each side and embedded in the substance of the broad ligament. They were well developed, 370 μ in diameter on an average, but their lumena contained no spermatozoa. More detailed description of the anatomy seems unnecessary in view of the excellent descriptions by Baker (1, 3) of similar cases.

The fixation in Bouin's fluid was good, but would have been better had the material been cut into pieces before fixation. Staining with Ehrlich's haematoxylin and eosin, Pasini or van Gieson gave good results.

Structure of the gonads

The ovarian portion of the ovotestes of pigs always occurs in a definite position in relation to the testis and epididymis. It is invariably situated on the pole of the testis next the angle of the epididymis. Accordingly this region of both gonads was sectioned as well as other parts. No ovarian tissue nor any oocytes could be found in the left gonad which was otherwise identical in structure with the right. The following description, with this reservation, applies equally to both gonads.

The major part of each gonad consists of a central testis surrounded by a well-developed tunica albuginea of fibrous connective tissue, which is, in many places, 80 to 110 μ thick. This central spermatic tissue consists of numerous lobules separated by connective tissue trabeculae in which the larger vessels run (Plate II, fig. 5). Each lobule is composed of numerous small tubules lined by a simple epithelium which obliterates the lumen and exhibits no signs of spermatogenesis. Quantities of large glandular interstitial cells in islets and strands, and a connective tissue network with capillaries, fill up the interstices between the tubules.

Outside the thick tunica albuginea is a narrow cortical zone of tissue which surrounds the entire gonad except in the region of the hilum. The greater part of this zone is composed of spermatic tissue with tubules resembling those in the medulla, interstitial cells, etc. This testicular cortex attains a thickness of 550 μ in places (Plate II, fig. 2) and is surrounded by a thin fibrous connective tissue layer, forming a poorly developed tunica albuginea about 10 μ thick. At the pole next the angle of the epididymis this testicular cortex in the right gonad passes into a patch of ovarian tissue about 2·5 mm. in diameter, and 1·25 mm. thick, which is composed of typical ovarian stroma containing many small oocytes in primordial follicles (Plate II, figs. 1 and 4). No large follicles or corpora lutea are present. The external tunica thins out and merges with the

fibrous stroma in this region, and it is covered by a cubical peritoneal or germinal epithelium, which does not extend over the spermatic portion. The chief or medullary tunica extends beneath the ovarian region, between it and the central testis (Plate II, fig. 4), but is here somewhat broken and less distinct than in other places. The transition zone between the ovary and the cortical spermatic tissue is intermediate in character and contains ovarian stroma and tubules with oocytes in them (Plate II, fig. 3).

The ovary passes over on one side into the fibrous tissue of the hilum containing the rete testis, vascular supply and lymph lacunae.

The left gonad is identical in structure except that the cortex is entirely spermatic in character, no ovarian tissue having been discovered, even in the most likely region.

The medullary region. The lobules of the medulla measure about 1 mm. in diameter and are separated by stout trabeculae of fibrous connective tissue, often 50μ in thickness, which are well supplied with blood vessels. The tubules (Plate II, fig. 5) in the lobules are small and convoluted; they measure about 50 to 70μ in diameter on an average. Each has a thin, but distinct, connective tissue basement membrane and a lining of a single layer of epithelial cells, the cytoplasm of which completely fills the lumen of the tubule. These cells occasionally exhibit mitoses, are not distinguishable into sertoli cells and spermatogonia and never exhibit prophase stages. Their nuclei are more or less oval in shape and their outline is somewhat irregular. The tubules in the different parts of the medulla are all in the same stage of development.

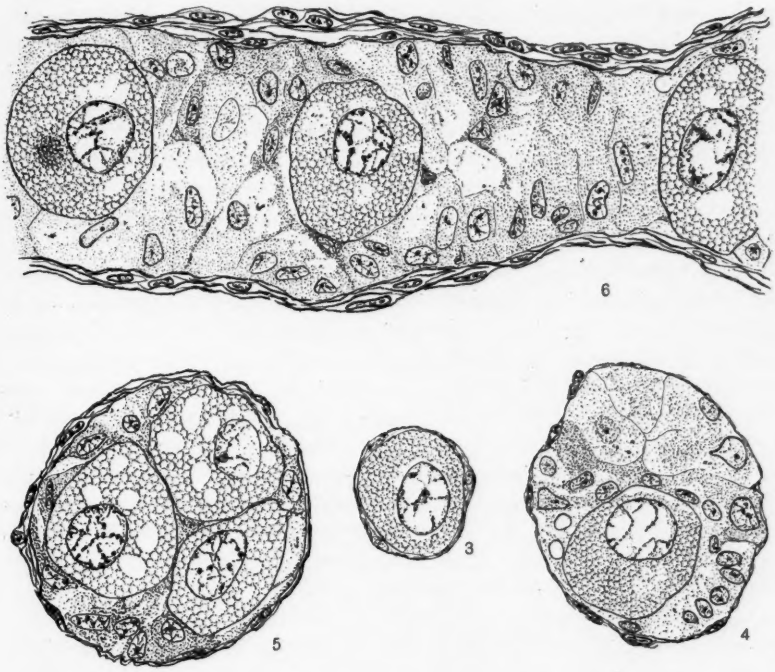
The interstitial cells are large and glandular in appearance and stain densely. They are roughly polygonal in shape and the nuclei are usually eccentric. The illustration (Plate II, fig. 5) shows that they are very plentiful and fill up the interstices in the fine network of connective tissue which occupies the spaces between the tubules. Both tubules and interstitial cells are of the type commonly found in undescended testes.

The tunica albuginea surrounding the medullary region is dense and thick. It is composed of fibrous connective tissue and is similar to that surrounding a normal testis (Plate II, figs. 2 and 4).

The ovarian cortex. The stroma in the deeper portions of the ovarian tissue is dense and fibrous and contains numerous lymph lacunae. The more superficial stroma is less fibrous and some of the cells are epithelial in appearance. It is well supplied with capillaries and lymph lacunae. Its surface is covered by a cubical peritoneal epithelium similar to that of a normal ovary. Numerous oocytes are present in primordial follicles consisting of a few flattened epithelial cells. They are localised chiefly in the superficial region, and are less frequent in the deeper parts (Plate II, figs. 1 and 4). These oocytes range from 25 to 35μ in diameter and therefore have not entered on the growth stage. They are normal and healthy in appearance with smooth cytoplasm and plump nucleus. The nuclei of the majority have attained the typical resting stage of the prophase of the heterotypic division. Some of the nuclei, however, exhibit

polarised loops which have not yet been transformed into the reticulum of the resting stage. No larger oocytes or follicles are present.

The ovarian region merges gradually with the testicular cortex. The transition zone presents some of the characters of both the testicular and ovarian regions of the cortex. It is composed of stroma similar to that of the ovary and of tubules and follicles interspersed with each other. The interstitial cells are not plentiful in this region. The follicles contain normal oocytes



Text-figs. 3–6. Drawn with the aid of a camera lucida. × 600. Fig. 3 shows an oocyte in a normal primordial follicle from the ovarian region. Figs. 4 and 5 show oocytes in enlarged follicles resembling tubules from the intermediate zone between the ovarian and spermatic portions of the cortex. Fig. 6 is from this zone also and shows three oocytes in a spermatic tubule.

similar to those in the truly ovarian tissue (text-fig. 3). The tubules are indistinguishable from those in the definitely spermatic region of the cortex. Many of the tubules in the immediate vicinity of the ovarian tissue contain scattered oocytes (Plate II, fig. 3). These oocytes occurring actually in the tubules (text-fig. 6) are exactly similar to those in the ovarian cortex and some of them also exhibit polarised chromatinic loops in the nuclei. These oocytes present a definite and distinct outline and nucleus. Their nature is quite indisputable and they cannot be confused with the deceptive ovum-like

bodies described by Crew and Fell (7), and said to be formed by a process of colloidal degeneration. Moreover, stages can be found in this region in which oocytes occur in "follicles" which are intermediate in structure between the tubules and the primordial follicles (text-figs. 4 and 5). The oocytes in tubules are strictly limited to this narrow transition zone between the ovarian and testicular cortex (Plate II, fig. 4).

The peritoneal epithelium rapidly thins and disappears over the transition zone and its place is taken by the thin cortical tunica albuginea which is continuous with the ovarian stroma and which surrounds the testicular cortex, merging with the thicker medullary tunica albuginea only in the region of the hilum where no cortex is developed.

The testicular cortex. The thin testicular cortex varies considerably but attains a thickness of 550 μ at the pole of the gonad farthest from the ovarian region. The tubules are similar to those in the medulla in structure except that the cytoplasm of the lining epithelium is less dense and more vacuolated (Plate II, fig. 2). The nuclei of these cells are similar to those in the medullary tubules in size and appearance and in the way they are arranged in a single layer near the wall of the tubule. They occasionally exhibit mitoses but never enter on the heterotypic division. The majority, if not all, of these tubules open on the peritoneal surface of the gonads by distinct pores (Plate II, fig. 2). These pores perforate the thin cortical tunica albuginea and the wall of the tubule. Sometimes they open directly into a tubule, when it is near the surface, and sometimes by a short but distinct canal (Plate II, fig. 2). The pores are quite distinct and may be marked either by a small extrusion of, or a hollow in, the contents of the tubule. The margins of the pores are clear cut and distinct in some instances, and ragged in others. Their definite structure and regular appearance preclude the possibility of their artificial formation during fixation or the subsequent treatment. The tubules branch and ramify in the cortex and are frequently more or less perpendicular to the surface; some, however, lie close to and parallel with it. This arrangement results in their being cut longitudinally more frequently than the tubules in the medulla and they consequently appear longer.

The tissue between these tubules is composed of loose fibrous connective tissue, containing many capillaries, lymph lacunae and strands and groups of interstitial cells. The latter are apparently identical with those in the medulla, but are not so numerous or so densely packed. The tubules are never grouped in lobules at the periphery, but incipient lobules are seen occasionally in the deeper layers immediately outside the medullary tunica or even forming islets surrounded by it. Such lobules are indistinguishable from those in the medulla.

III. DISCUSSION

Morphological significance

The gonads described in this paper are chiefly of interest because of the light they throw on the origin and development of hermaphroditism. The presence of a medulla and cortex, separated by a tunica albuginea, is one of their most remarkable characteristics. Baker (1) evidently observed a similar arrangement, since he notes and figures the occurrence of spermatic tubules outside the tunica albuginea in intersexual pigs. It must be assumed that the medulla represents the testis of a normal male, and that its tubules have been derived from the first or medullary cords proliferated during embryonic life from the germinal epithelium. The tunica albuginea surrounding the medulla must be homologous with that surrounding the normal testis and therefore represents the primitive tunica albuginea of the embryonic gonad which persists in the male but disappears in the female. The zone outside this tunica will, on these assumptions, be homologous with the cortical cords which form the cortex of the ovary but do not develop in the normal male. This zone obviously has been arrested at an early stage and has never attained as full a development as in the normal ovary. The small ovarian portion alone has completed its differentiation and produced typical ovarian tissue. The tubules composing the remainder of the cortex do not resemble any structures occurring in a normal gonad. They are, however, almost identical with the tubules in the medulla, and are similar to those in many descended (Baker (2)) and undescended testes of sex intergrade pigs. This similarity, despite the absence of spermatogenesis, appears to warrant calling them spermatic tubules. Their structure and distribution clearly suggest that they have been derived, with comparatively little modification, from cortical or Pflügerian cords which had not differentiated into definitely ovarian structures. Such an explanation is supported by their persistent superficial attachment, which resembles that of the cortical cords before they have become detached from the embryonic germinal epithelium. The pores by which they open to the exterior possibly represent the persistent remains of the cavities of the hollow invaginations of the germinal epithelium which constituted these cords or tubes of Pflüger. It is, however, impossible to deny that these pores may have been formed by a secondary perforation or erosion of overlying tissue, in which case they would not be comparable to the original cavities of the cortical cords.

This hypothesis also serves to explain the intermediate stages between tubules and follicles which occur in the transition zone between the ovarian and spermatic portions of the cortex. Oocytes occur in this zone in normal follicles, in tubules and in enlarged follicles which are intermediate in character. Apparently the cords in this region developed oocytes but did not differentiate completely into follicles, as in the ovarian region. Consequently some of the oocytes remained in tubules and others became included in normal follicles or abnormal ones of intermediate character. This explanation emphasises the

fundamental homology between spermatic tubules and ovarian follicles, and accounts for the close approximation in appearance between sterile spermatic tubules and anovular follicles. The structure of the oocytes in these tubules is not obviously degenerate and does not admit of their dismissal as products of colloidal degeneration (Crew and Fell (7)).

The spacial relations of the ovarian and testicular tissue in ovotestes of pigs are constant in all cases described, irrespective of the relative development of the two parts. Baker (3) describes this accurately in stating that the ovarian tissue is situated on the ventro-antero-median surface of the testis, and remarks that "apparently the corresponding part (*whichever that may be*) of the embryonic gonad gives rise to ovarian tissue more readily than the remainder." It is extraordinarily difficult to identify the true morphological position of these parts since the gonad undergoes unequal growth and rotation in relation to the adjacent structures during development. It is, however, known that the anterior end of the embryonic gonad exhibits a more advanced stage of development than the posterior and that the cortex is more developed ventrally than laterally. It would be reasonable, therefore, to suppose that the antero-ventral surface of the embryonic gonad would give rise to the ovarian part of the ovotestis.

It is remarkable that a definite epithelium, while present over the ovarian portion, is absent from the spermatic regions of the gonads described. Moreover, the latter have a distinct, although thin, tunica albuginea covering them. Evidently the retention of the germinal epithelium and the development of the tunica albuginea are effected in direct response to the immediately underlying tissues. An exactly similar arrangement has been described in the ovotestis of a pigeon in process of sex-reversal (Brambell and Marrian (5)). The tunica albuginea surrounding the spermatic portions of the cortex is homologous, presumably, to the secondary tunica of the embryonic ovary which persists in the normal female.

The sterile condition of the spermatic tubules of these gonads requires mention. This condition is commonly found in undescended testes but Baker (2) has described it also in the descended testes of sex-intergrade pigs. It is probable, therefore, as has been suggested by Crew (8), that this condition does not merely result from non-descent.

Developmental origin

Crew (8) has made an elaborate attempt at explaining hermaphrodite and intersexual pigs by means of a modification of Goldschmidt's theory of Lymantria intersexes. It is unnecessary to discuss his hypotheses in detail, but the fundamental conception of a time factor, involved in the appearance of the stimuli effecting differentiation of sex, has a special application in the present case. While acknowledging the origin of this conception the author is responsible for its application in this particular case.

At the time when sexual differentiation normally takes place the embryonic

gonad consists of the medullary cords surrounded by the primitive tunica albuginea and the germinal epithelium. The testes differentiate positively before the ovaries, the medullary cords transforming into the spermatic tubules, the primitive into the definitive tunica albuginea, and the germinal epithelium degenerating. The ovaries, which are at first distinguishable only by comparison with testes of the same age, soon exhibit a renewed activity of the germinal epithelium resulting in the proliferation of the cortical or Pflügerian cords. The growth of the cortical cords soon results in the disruption of the primitive tunica albuginea and the compression and partial degeneration of the medullary cords in the centre. It is probable that, in some mammals at least, a third proliferation takes place in the differentiated ovary shortly before puberty (de Winiwarter and Sainmont (10)). It is therefore necessary to assume that in a male the stimulus determining the differentiation of the testes is effective almost immediately after the completion of the medullary proliferation. Delay in the appearance of this stimulus would presumably result in the formation of the cortical cords in a peripheral zone around the gonad. These cords always exhibit more advanced development anteriorly and ventrally than posteriorly and laterally. A stage would then be reached when the cortical cords at the antero-ventral end of the gonad had partially disrupted the primitive tunica albuginea and had definitely differentiated into ovarian tissue. The remainder of the cortical proliferation would not have differentiated and would still be outside the primitive tunica albuginea. If it is assumed that the delayed male stimulus became operative at this time, it would be expected to transform the medullary cords and indifferent cortical cords into spermatic tubules and to cause the remains of the primitive tunica albuginea to persist, while having no effect on the already differentiated ovarian tissue. It would also account for the intermediate character of the narrow zone containing oocytes in tubules, and for the invariable occurrence of the ovarian tissue at one pole of the testis and divided from it by a more or less intact tunica albuginea. It is interesting that a stage resembling this condition actually occurs normally in the male mouse embryo, but is transient. Immediately after the testes have differentiated, the germinal epithelium proliferates and forms a thin zone outside the primitive tunica albuginea (Brambell (6)), which is homologous with the cortical proliferation of the ovary. This incipient cortex soon ceases to develop and disappears without ever differentiating at all. The condition, though transient, is comparable to the hypothetical stage required to explain hermaphroditism in the pig.

It is remarkable that in the pig ovotestes the ovarian portion usually contains oocytes and is comparatively normal, whereas the spermatic tubules are invariably sterile and show no indications of spermatogenesis. Apart from this phenomenon the two tissues are mutually compatible and appear to remain permanent constituents of the gonads.

The present example had an ovotestis on one side and a testis on the other. Other cases have been described with two ovotestes, an ovotestis on one side

and an ovary on the other, and with an ovary on one side and a testis on the other. Baker (3) has attempted to show a greater tendency of the left side to form an ovary or ovotestis, and of the right a testis or ovotestis. The number of cases recorded are, however, insufficient to warrant any conclusion. The hypothesis advanced in this paper would appear to require a slight variation in the time of development of the gonads on the two sides to account for those cases in which the two gonads differ in their constitution.

Accessory organs

The presence of both ovarian and testicular tissue seems to account sufficiently for the intersexual character of the accessory organs in hermaphrodite pigs, since the development of these organs is controlled by hormones from the gonads. Crew (8) states that hermaphrodite pigs with an ovary on one side develop the epididymis and vas deferens on the other side only, whether this gonad is a testis or ovotestis. He points out that this indicates that the epididymis and vas deferens require some direct stimulus, not a hormonal stimulation alone.

Genetic origin

The fact that certain strains of pigs are much more prone to hermaphroditism and intersexuality has been observed a number of times (Baker (3, 4), Crew (8), etc.). This suggests, as Crew has pointed out, that genetic factors are involved in their production.

IV. SUMMARY

1. The reproductive organs of an hermaphrodite pig are described. The right gonad was an ovotestis and the left was a testis. Both gonads consisted of a medulla of spermatic tissue surrounded by a well-developed tunica albuginea and, outside this, a cortical zone of spermatic tubules. The ovarian tissue composed a small part of the cortical zone of the right gonad.

2. The spermatic tubules of both cortex and medulla were sterile. Those of the cortex opened by distinct pores on the surface of the gonads. Interstitial tissue was plentiful.

3. The ovarian tissue was normal and contained numerous small oocytes in primordial follicles. The region of the cortex between the spermatic and ovarian regions was intermediate in character. Many of the tubules in this region contained true oocytes.

4. The ovarian tissue was covered on the outside by a cubical epithelium which was absent from the spermatic regions of the cortex, its place being taken by a thin secondary tunica albuginea.

5. The structure of these gonads can easily be explained embryologically by postulating a slight delay in the appearance of the male determining stimulus.

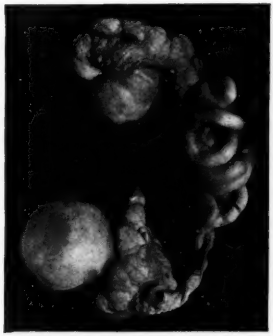


Fig. 1.

Fig. 2.

Fig. 3.

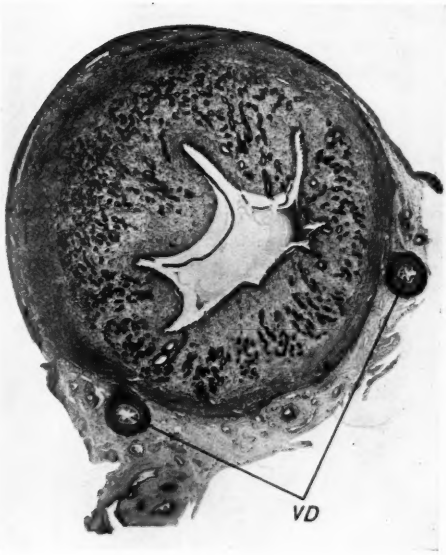


Fig. 4.

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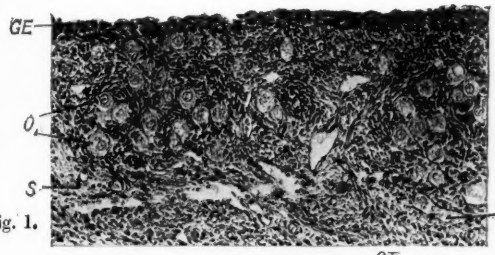

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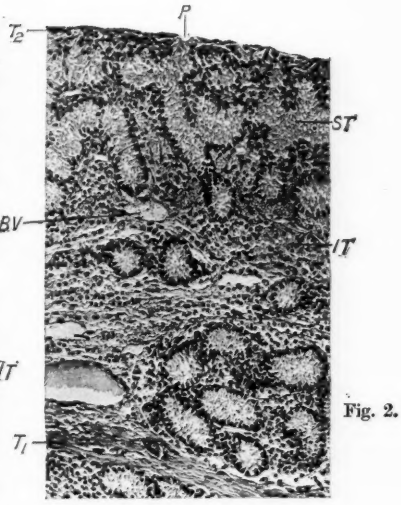

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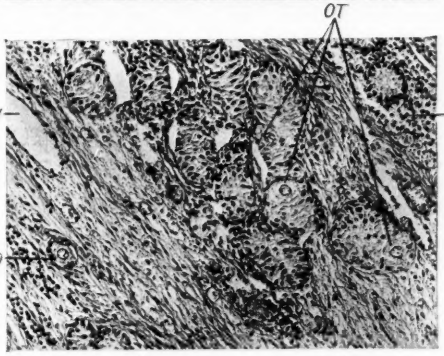

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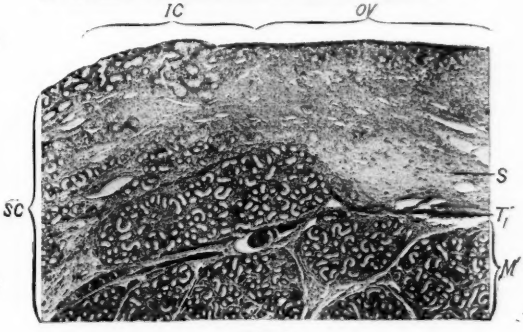

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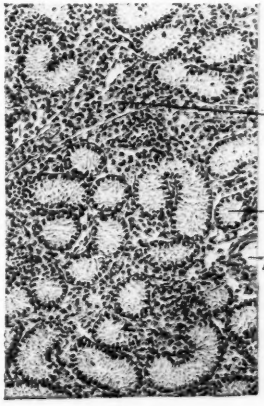

Fig. 5.

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DESCRIPTION OF PLATES I, II

Guide Letters

BV. Blood vessel. *GE.* Germinal epithelium. *IC.* Intermediate zone of cortex. *IT.* Interstitial tissue. *M.* Medulla. *O.* Oocytes. *OT.* Oocytes in tubules. *OV.* Ovarian zone of cortex. *P.* Peritoneal pore of cortical spermatic tubule. *S.* Ovarian stroma. *SC.* Spermatic zone of cortex. *ST.* Spermatic tubule. T_1. Primary tunica albuginea. T_2. Secondary tunica albuginea. *VD.* Vas deferens.

Plate I

Figs. 1 and 2. Dorsal and ventral aspects of the organs described. The upper gonad is the right and the lower the left in both figs. $\frac{2}{3}$ nat. size.

Fig. 3. Section of portion of left epididymis. × 27.

Fig. 4. Section of medial uterus showing well-developed uterine mucosa with glands and the two vasa deferentia in the broad ligament. × 14.

Plate II

Fig. 1. Ovarian region of cortex, showing germinal epithelium and oocytes in primordial follicles embedded in typical stroma. × 100.

Fig. 2. Spermatic region of cortex, showing tubules opening to the surface, interstitial cells and the thick primary and very thin secondary tunica albuginea. × 100.

Fig. 3. Intermediate zone of cortex, showing oocytes in tubules and one in a primordial follicle. The ovarian nature of the stroma and the interstitial cells are also shown. × 100.

Fig. 4. Ovotestis, showing ovarian, intermediate, and testicular regions of cortex, and the primary tunica albuginea surrounding the medulla and including in it one large lobule of spermatic tissue. × 20.

Fig. 5. Medullary region of ovotestis, showing spermatic tubules and interstitial tissue. × 100.

The author is indebted to Mr D. A. Kempson for the photographs reproduced in Plate I, figs. 1 and 2, and to Mr F. J. Pittock for the photomicrographs.

THE DISTINCTIONS OF THE HUMAN HALLUX

By FREDERIC WOOD-JONES
Honolulu

TEN years ago, when dealing with the distinctions of the human foot as compared with the foot of the anthropoid apes, I had occasion to refer to some statements made by Huxley in *Man's Place in Nature*. The point at issue was the range of movements of which the first pedal digit is capable in man and in the apes. In the process of showing that there was a very real difference between man and apes in this regard, a difference which, to my mind, had been minimised by Huxley, I laid emphasis upon the distinctions of the human foot even in the early stages of its development. Since that paper was written a great deal of detailed work has been done upon the ontogeny and phylogeny of the human foot with a view to establishing its pithecoid origin (see (3, 4, 5, and 7)), and to-day there seems to be some danger that we may be lulled into thinking that the comparatively recent "transformation of the foot of a gorilla into that of a man" is one of easy and actual accomplishment.

Huxley, in many statements, created a belief that the differences between the foot of a gorilla and that of a man were slight and unimportant. In particular he attributed to boot-wearing the human limitation of movements of the big toe. The statement that I criticised was: "It must not be forgotten that the civilised great toe, confined and cramped from childhood upwards, is seen to great disadvantage, and that in uncivilised and barefooted people it retains a great amount of mobility, and even some sort of opposability." From that statement Huxley continues by citing the examples of the Chinese boatmen, Bengalese weavers and thieving Carajos that I criticised in 1918.

Briefly, I contended that boot-wearing accounted for none of the distinctively human features of the foot and that, although mobility of the great toe is more highly developed in unbooted races and in little children, it never manifests itself in any sort of opposability and never approaches the type of movement characteristic of the Anthropoids. These are plain facts of observation of the movements of which men and apes are capable; and it was urged that they have as their basis the simple anatomical facts that the human first metatarsal is (1) articulated to the entocuneiform by a flat and not by a concavo-convex facet and (2) is bound to the other metatarsals distally as well as proximally by strong ligaments, the distal binding of the transverse metatarsal ligament being its human distinction.

In 1920(1) Gerrit S. Miller, though strongly dissenting from some of my views, supported wholeheartedly the contentions as to the distinctions of the

human foot and he especially dwelt upon the differences between the movements of the human and gorilloid big toe. In particular he drew attention to the finding of Leboucq (1882) that even in the human embryo of 21 mm. the tarso-metatarsal joint is typically flat; and that human big toe movements involve the metatarso-phalangeal joint, whereas in the Anthropoids, as in the human thumb, the tarso-metatarsal joint is involved. Two statements may be quoted from Miller's paper: (1) "the basal joint of the human hallux appears to be free from gorilloid taint at every stage of its development"; (2) "the principal motion involves the phalanges only, and not, as in the apes, the entire digit to the base of the metatarsal" (p. 238).

These statements were not destined to pass unchallenged and to-day the subject seems to be reinvolved in unnecessary uncertainty. In 1922 and 1924 (2) Dr Dudley J. Morton contributed an extended study on the "Evolution of the Human Foot." He dissented from the teaching that the transverse metatarsal ligament acted in the way that all human anatomists have been agreed upon and he also dissented from the usual anatomical description of it to which Miller and I had appealed.

Dr Morton states: "Through the courtesy of Professor Ferris of the Yale Medical School, the writer found by dissection that the transverse ligament of the human foot, to which Mr Miller refers, completely binds only the second, third, fourth and fifth metatarso-phalangeal joints, with merely an extension toward the hallucial joint. This finding was verified in a second dissection and is shown in the accompanying illustration. The transverse ligament, as it is followed inwardly from the fifth digit, begins from the outer side of the latter as a definite fibrous flattened band, crossing the bases of the proximal phalanges and receiving fibers from their joint structures; at the inner border of the second digit it divides, sending an important bundle dorsally along the inner side of this digit to fuse with its fibrous joint structure. The other portion extends its fibers radially into the intervening soft superficial structures between the bases of the first and second digits. This extension does not include nor cross the phalanx of the hallux as it does that of the fifth digit, nor does it show any attachment to the hallux except indirectly through the structures into which it extends. These findings clearly indicate that the fibers, which are projected towards the hallux, are of comparatively recent development and formed to include the hallux, which at an earlier period had been capable of a considerable degree of abduction" (1922, p. 330).

Dr Morton's figure is reproduced here, and it will be noted that the ligament dissected appears to be immediately subcutaneous and to lie superficial to the flexor tendons and their sheaths. That this figure represents, in a diagrammatic way, the transverse fibres of the plantar fascia ("fasciculi transversi" of Zuckerkandl, "bandelette transverse souscutanée des orteils" of Bourgery, "ligt. palmant interdigital" of Poirier, "ligt. natatorum" of Grapow, "ligt. interdigitaux" of Juvara, or "superficial transverse ligt. of the toes," and "interdigital ligt." of English authors) seems obvious; and this assumption

appears to be verified by the description of some of its fibres extending to "the intervening soft superficial structures between the bases of the first and second digits." Obviously the disposition of this trivial superficial fascial band—although as a fact it usually connects all the toes—has no bearing whatever on the action of the transverse metatarsal ligament to which alone both Mr Miller and I referred.

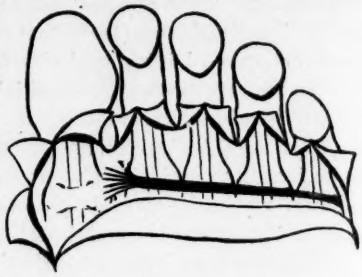

Fig. 1. Dr Morton's illustration of the ligament described in the text. (Reproduced by kind permission from the *American Journ. Phys. Anthropology*, vol. v, no. 4, 1922.)

As for the facet on the entocuneiform, Straus (6) (1927) has verified the findings of Leboucq in the human embryo in which it is flat even in the youngest stages. But Straus adds, "we must remember, however, that until we are able to examine the condition of this joint in early gorilla and other Anthropoid foetuses, we cannot draw any sound conclusions regarding its contour in the ancestral type of the higher primates" (p. 118). This would seem to be almost unnecessary scientific caution since we know its concavo-convex form in all living primates higher and lower, and its definite establishment in the Eocene *Notharctus*.

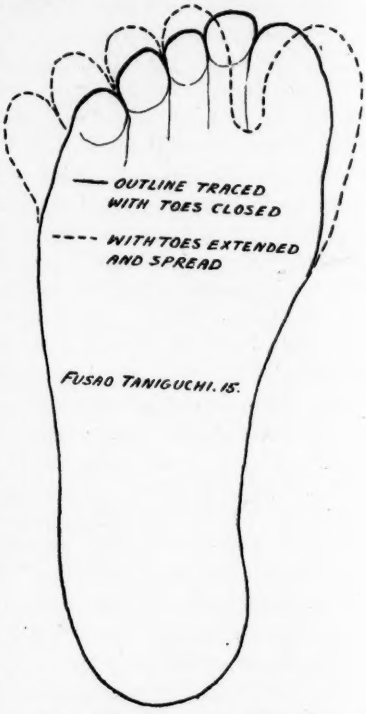

Fig. 2. Traced outline of the left foot of a congenitally armless Japanese boy.

It would be, perhaps, a retrograde step if these many recent contributions to the study of the human foot were to lead to the loss from sight of two very simple facts: (1) the extremely early ontogenetic human acquirement of definitely human pedal characters and (2) the vast difference in kind between the best human big toe movements and those habitual in the Anthropoid apes. With regard to the latter point I have waited to re-affirm my statements until it was possible to examine a case in which the human big toe movements were in a condition that all would agree was an optimum. In Honolulu the swarms of Japanese children go mostly barefoot, and, as Kohlbrugge remarked, if

the mobile big toe is to be considered as an ape-like feature "one would hardly dare in an anthropological congress held at Tokio to refer to it as a sign of inferiority." Mobility of the big toe is, therefore, a familiar condition; but I have been fortunate enough to meet a barefooted Japanese boy fifteen years old who was born without any arms. This boy can do most things with his toes and, like so many congenitally armless persons, aspires to earn his living as an artist. In this child the big toe can be abducted widely from the second toe and all the toes have a very unusual degree of co-ordinated control for fine movements: but, even to the most careful examination, there is revealed no independent metatarsal movement in the big toe, no power of rotation and naturally not the least trace of "some sort" of opposability. All movements take place by a high degree of flexion, extension, abduction, and adduction of the digits at the interphalangeal and metatarso-phalangeal joints: and this I think may be regarded as a maximum human attainment.

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CRANIOMETRIC MEMOIRS

No. I. THE PROPORTION BETWEEN THE NASION-ALVEOLAR HEIGHT AND THE NASAL WIDTH: A NEW CRANIAL INDEX, AND ITS SIGNIFICANCE

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So far as the writer can ascertain, this cranial index has never been previously described. One of its factors, the nasion-alveolar height, is usually termed by craniologists the upper facial height, in contradistinction to the complete facial height, as measured from the nasion to the menton. The writer therefore decided to ascertain the exact relation which the width of the anterior nasal aperture of the skull bore to the upper facial height. As the latter is the longer of these two cranial measurements, the index is obtained from the following formula:

$$\frac{\text{Nasal width} \times 100}{\text{Nasion-alveolar height}}.$$

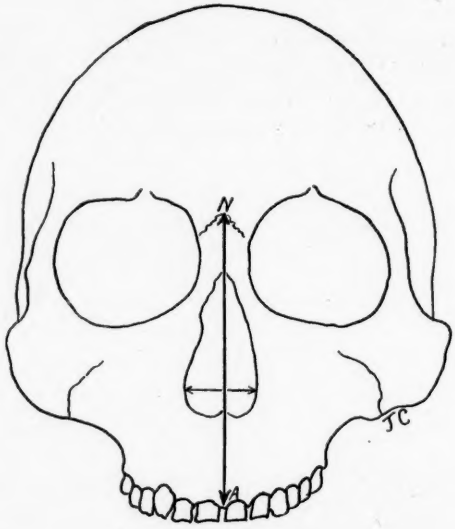

Fig. 1. The two factors concerned in the $\frac{\text{nasal width}}{\text{facial height}}$ index. Tracing from a photograph of male Eskimo skull XIV H4, Victoria Museum, Ottawa.

It should be mentioned at this stage that Pearson (7) has recently suggested a new method of localising the alveolar point. All the measurements utilised by the present writer were, however, those made by Hrdlička (4, 5, 6) and Turner (8) from the ordinary alveolar point or prosthion.

This index suggested itself first of all to the writer while he was engaged in making his Report (1) to the Dominion Government on the Eskimo crania of the Canadian Arctic Expedition, 1913–1918. It is important to mention that these were representative of the Central and Western Eskimos. He found that the average $\frac{\text{nasal width}}{\text{facial height}}$ index for the male crania was 29·4, the interpretation of which was that the nasal width was, on the average, 29·4 per cent. of the nasion-alveolar height in that cranial group. On investigating the index in the female crania, however, he found that its average was slightly higher than in the males, namely 31·2. This suggested of course the existence of a sexual factor, but he did not make mention of this fact in his report, seeing that the numbers of crania that were available for examination were comparatively small, namely eleven male and fifteen female. It may therefore be mentioned at the very outset of this paper that the present investigation confirmed the existence of this sexual factor, not only in the Eskimo, but also in all the other racial types, which, as shown in the list below, were not only very diverse in character, but also fairly representative of mankind in general.

It is important to state here that the term "facial height," which will be used constantly throughout this memoir, will in all cases refer to the *upper* facial height.

All the measurements of the nasal width and the facial height that were utilised to calculate this index were taken from Hrdlička's three recently published catalogues (4, 5, 6), with the exception of those for the Scottish crania, which were obtained from Turner's memoir (8). The numbers that were studied are shown in the subjoined table:

	Males	Females
Eastern (Greenland) Eskimo (U.S. N. Museum)	35	32
Western (St Lawrence Island) Eskimo (U.S. N. Museum)	50	50
Mongol crania (U.S. N. Museum)	50	50
Arikara American Indian (U.S. N. Museum)	51	42
Scottish crania	67	31
American Negro (U.S. N. Museum)	22	12
Australians (Southern Territory)	50	50
Tasmanians	15	14
	340	281

RANGES OF VARIATION OF THE $\frac{\text{NASAL WIDTH}}{\text{FACIAL HEIGHT}}$ INDEX

This index was found to display the usual wide ranges of variation that are exhibited by all cranial measurements and indices. It was interesting to note that the narrowest ranges were exhibited by the Eskimo crania, particularly by those from the Eastern or Greenland Area. It is important to mention that in several recent papers the writer has directed attention to the narrowness

of the ranges that are displayed by the cranial measurements and indices of this racial group. The explanation is an interesting one, for it indicates that the Eskimo race is comparatively homogeneous in character, and therefore remarkably free from racial admixture. One would naturally expect this condition of matters to exist as a direct result of their geographic position, which would render them less liable than most races to the infusion of foreign blood. It therefore proved of interest to compare these Eskimo ranges of variation with those exhibited by some of the other races shown in Tables I and II. For example, the range for the index in the Greenland Eskimo female crania was from a maximum of 36·3 to a minimum of 26·3, the actual range being thus only 10·0. In the Australian female crania, on the other hand, the index exhibited a range of as much as 19·8, that is to say, almost twice as much as that for the Greenland Eskimo female crania. A survey of Tables I and II shows that the ranges of variation tended to be highest in the Negro racial groups, this feature being displayed by both the male and the female crania.

Table I.

The ranges of variation of the $\frac{\text{nasal width}}{\text{facial height}}$ index are lowest in the Greenland Eskimo, and tend to be highest in the Negro races. In this table the results for the male crania are alone shown.

	Minimum	Maximum	Range of variation
Greenland Eskimo (U.S. N. Museum)	26·5	37·6	11·1
St Lawrence Island Eskimo (U.S. N. Museum)	26·1	40·0	13·9
Mongol crania (U.S. N. Museum)	28·9	43·2	14·3
Arikara American Indian (U.S. N. Museum)	28·1	39·7	11·6
Scottish crania	28·0	44·2	16·2
American Negro (U.S. N. Museum)	32·8	45·9	13·1
Australian Aboriginal	32·3	47·7	15·4
Tasmanian Aboriginal	29·1	48·3	19·2

Table II.

The ranges of variation of the $\frac{\text{nasal width}}{\text{facial height}}$ index are lowest in the Greenland Eskimo, and tend to be highest in the Negro races. In this table the results for the female crania are alone shown.

	Minimum	Maximum	Range of variation
Greenland Eskimo (U.S. N. Museum)	26·3	36·3	10·0
St Lawrence Island Eskimo (U.S. N. Museum)	28·4	40·0	11·6
Mongol crania (U.S. N. Museum)	31·0	45·4	14·4
Arikara American Indian (U.S. N. Museum)	27·5	42·1	14·6
Scottish crania	25·6	38·8	13·2
American Negro (U.S. N. Museum)	31·8	46·6	14·8
Australian Aboriginal	33·3	53·1	19·8
Tasmanian Aboriginal	35·8	48·2	12·4

THE STANDARD DEVIATIONS OF THE $\frac{\text{NASAL WIDTH}}{\text{FACIAL HEIGHT}}$ INDEX

The numbers of crania that were available to represent the Tasmanians and the American Negro were relatively small in comparison with the other cranial groups. From previous experience in regard to this matter, the writer

judged that it would not be profitable to study the standard deviations and coefficients of variability of the index in these two races. As a result the errors of the mean for the Tasmanian and the American Negro crania were not available. The standard deviations were studied in all the other racial types, namely, in both Eskimo groups and in the Mongol, the American Indian, the Australian and the Scottish crania.

The standard deviations were found to follow the ranges of variation more or less consistently. They were therefore lower, on the whole, in the two Eskimo cranial groups than in the others. The converse was also true, for it may be noted from Table III that the standard deviations were highest in the Mongol and in the Australian crania which, as Tables I and II show, exhibited also wide ranges of variation. The standard deviation was also rather high in the case of the female Scottish crania, certainly in comparison with the male crania. It may be likewise observed from Table III that the coefficients of variability followed the standard deviations more or less consistently.

Table III.

The standard deviations of the $\frac{\text{nasal width}}{\text{facial height}}$ index followed the ranges of variation more or less consistently. That is to say, they tended on the whole to be low in the two Eskimo groups and rather high in the Mongol and Australian crania (compare with Tables I and II).

	Males		Females	
	S.D.	C. of V.	S.D.	C. of V.
Greenland Eskimo (U.S. N. Museum)	2·86	9·22	2·77	8·93
Western Eskimo (U.S. N. Museum)	2·77	8·52	2·32	6·86
Mongol (U.S. N. Museum)	3·14	8·87	3·04	8·30
American Indian (U.S. N. Museum)	2·75	7·99	2·83	8·03
Australian Aboriginal	3·07	7·95	3·58	9·24
Scottish crania	2·85	8·82	3·36	10·21

THE AVERAGE $\frac{\text{NASAL WIDTH}}{\text{FACIAL HEIGHT}}$ INDEX IN THE GREENLAND ESKIMO

The index was found to reach its lowest ebb in this racial group, the average for the males being as low as 31·00. The standard error of the mean was calculated to be $\pm$ 0·3263. It was thus interesting to learn from the index that the nasal width was, on the average, only 31 per cent. of the facial height in these Greenland Eskimo males. This lowering of the index was found to be mainly due to narrowing of the nasal aperture which is such a feature of the Eskimo, particularly those tribes from the Eastern Area. For instance, the present writer in his Report (1), referred to above, states that "his contracted nasal aperture, which is perhaps his most important cranial specialisation, places the Eskimo skull in a category by itself. It will probably be granted by most observers that this modification can be explained by his climatic environment. The inhaling for prolonged periods of cold air, frequently registering many degrees below zero, would most assuredly compel nature to design and

provide as narrow an aperture as possible, so as to reduce the chilling effect of this intensely low temperature to a minimum."

The average $\frac{\text{nasal width}}{\text{facial height}}$ index for these female Greenland Eskimo crania was fractionally higher than in the males, namely 31·11. The error of the mean in this instance was calculated to be ± 0·3304. This raising of the index in the females, slight though it was, thus confirmed the results obtained by the writer in the Eskimo crania of the Canadian Arctic Expedition, though in the present instance the sexual difference was more than offset by the error of the mean. Unfortunately the numbers of Greenland Eskimo crania that were available in Hrdlička's catalogue (4) consisted of only thirty-five males and thirty-two females. It would obviously require far greater numbers than these to bring out the full effects of the sexual factor, so that we shall have to be satisfied for the present with the small sexual difference that was found, fractional though it be.

The writer was fortunately able to devise another plan to demonstrate the existence of this sexual factor. Of course when comparing measurements of the male skull with those of the female skull, one would naturally expect them to become, as a general rule, definitely shorter in the latter. He found that, on comparing the average facial height of the Greenland Eskimo female crania with that of the male crania, the female average exhibited a reduction of 7·1 per cent. On the other hand, the amount of reduction of the average nasal width in the female crania from that of the males was found to be definitely less, namely 6·2 per cent. That is to say, the average nasal width in these female Greenland Eskimo crania approximated more to the average for the males than did the average for their facial height (see Table VI). There could thus be no dubiety regarding the existence of a sexual factor, the deliberate effect of which would be to increase the $\frac{\text{nasal width}}{\text{facial height}}$ index in the female crania. It may be mentioned at this stage that this same sexual factor was found to exist definitely in all the other racial groups that were examined in connection with this research (see Table V).

THE AVERAGE $\frac{\text{NASAL WIDTH}}{\text{FACIAL HEIGHT}}$ INDEX IN THE WESTERN ESKIMO

These Eskimo crania were so named because they came from the Western Eskimo Area, the term Central Area being usually applied to those regions situated to the north of Canada, while the term Eastern Eskimo is usually applied to those tribes situated to the east of this, including of course the Greenland Area. The crania selected to represent the Western Eskimo came from St Lawrence Island, which is situated off the west coast of Alaska just south of the Bering Strait. The fifty male crania were those numbered 279453 to 279539, while the fifty female crania were from 279403 to 279512 in Hrdlička's catalogue (4).

The average index for the males was 32·5, the error of the mean being calculated to be ± 0·2642. Note that this average was definitely higher than that for the Eastern Eskimo male. This fact will be shown later to be of the greatest significance. The average index for these Western Eskimo females proved to be 33·8. The error of the mean in this case was calculated to be ± 0·2213. It may thus be noted that the index was definitely higher than in the males. In fact the sexual difference was nearly six times the amount of the error of the mean, and thus assumed a definite degree of significance. There could therefore be no question regarding the existence of the sexual factor in these Western Eskimos. It was indeed fortunate that there was such an abundant supply of St Lawrence Island Eskimo crania available for study.

The writer adopted a second plan to demonstrate the existence of this sexual factor, just as in the case of the Greenland Eskimos. Thus he found that the average facial height in these Western Eskimo female crania, when compared with that for the males, exhibited a reduction in amount of 8·3 per cent. On the other hand, he compared the amount of reduction of the average nasal width in the females from that of the males, and found it to be only 2·9 per cent. That is to say, the average nasal width in these Western Eskimo female crania approximated much more closely to the average for the males than did the average for their facial height (see Table VI). The obvious effect of this was to increase the $\frac{\text{nasal width}}{\text{facial height}}$ index very definitely in the female crania, as noted above and also in Table V.

It may be likewise noted that the index for the Western Eskimo females, like that for the males, was definitely higher than in the Eastern Eskimo female crania. This is a fact of great morphological importance, for it provides us with one more point of contrast between these two Eskimo tribal groups. Hrdlička (4) has shown that in the Eskimo "the cranial breadth, and with it the cranial (cephalic) index, decrease gradually from the west to the east. There is no sudden change at any geographical point, and as there has also been no known or even suspected coming in at any point of other people who would have admixed, and modified the Eskimo, the gradual change in head form may be regarded as having taken place within the tribes themselves, and is probably connected with environment conditions—using the term 'environment' in its broadest sense." In addition to this transformation of the cephalic index, the present writer (2, 3) has recently shown that the length-height and the breadth-height indices both undergo definite alterations as one proceeds from east to west or *vice versa* through the geographic Eskimo groups. We are now provided with a fourth cranial index that exhibits a remarkable change when one compares the Eastern with the Western Eskimo. The clue to these remarkable changes will be found when we come to study the Mongol crania.

THE AVERAGE $\frac{\text{NASAL WIDTH}}{\text{FACIAL HEIGHT}}$ INDEX IN THE MONGOL

These crania, which came from Urga in Mongolia, were represented by fifty males and fifty females. The male series was from 278794 to 278827 and the female from 278913 to 278733 in Hrdlička's catalogue (4).

The average index for the males was noted to be 35·4, the error of the mean being calculated to be ± 0·2995. The average index for the male Mongol thus exhibited a definite increase when compared with those for the Western and Eastern Eskimos. The average index for the female Mongol crania proved to be 36·6, the error of the mean in this instance being calculated to be ± 0·29001. One was thus enabled to record once more a higher index in the female than in the male crania of a racial group. Indeed, the sexual difference was more than four times the amount of the error of the mean in this instance, and thus gained a certain degree of significance. The evidence therefore pointed strongly to the existence of a sexual factor in the case of these Mongol crania.

The writer also demonstrated the existence of this sexual factor by means of the plan adopted in the case of the Eastern and Western Eskimos. Thus he noted that the average facial height of these female Mongol crania, when compared with that for the males, displayed a reduction amounting to 9·9 per cent. On the other hand, he studied the degree of reduction of the average nasal width in the females from that of the males, and found it to be definitely less, namely 6·9 per cent. That is to say, the average nasal width in these female Mongol crania approximated more closely to the average for the males than did the average for their facial height (see Table VI). This fact would explain the increase in the $\frac{\text{nasal width}}{\text{facial height}}$ index in the female, as contrasted with the index for the male crania.

We now come to one of the outstanding facts yielded by this investigation. It may be noted from Table IV that the indices are much higher in the Mongol than in the Eastern Eskimo crania, both male and female, with the indices for the Western Eskimo representing a sort of intermediate stage between the two racial groups. Of course it is a well-recognised fact that the Eskimo is Mongolian in origin. It is therefore of the greatest significance to note in Table IV that the indices for the Western Eskimo represent the transition stage between the Mongolian type of index and that found in the Eastern Eskimo, who by migration and subsequent environmental changes has become farthest removed, both morphologically and ethnologically, from his Mongolian ancestor. In this relationship it is important to quote what Hrdlička (4) states with reference to the Eskimo stock. Thus he says, "There is a plain connection of the stock with the Bering Sea and the Asiatic Eskimo, and through these with the mongoloid type of north-eastern and northern Asia." Further on he states, "The derivation of the Eskimo type from one like the Mongolian appears quite evident." In a recent study (2) of the length-height cranial index

the present writer states that "the male indices become definitely lowered in the Central and Western Eskimo groups, until they approximate to those for the Mongol crania." Again, in another recent paper (3) dealing with the breadth-height cranial index the present writer states that "the breadth-height index gradually diminishes from east to west through the various Eskimo geographic groups, until it finally approximates to that of the Mongol." To this testimony we are now able to add this new $\frac{\text{nasal width}}{\text{facial height}}$ index, together with the statement that it exhibits a definite increase in the Western as compared with the Eastern Eskimo. The former thus represents the phase of transition between the latter and his Mongolian ancestor, as shown in Table IV.

Table IV.

The $\frac{\text{nasal width}}{\text{facial height}}$ index in the Western Eskimo represents the transition stage between the index for the Eastern Eskimo and the index for his Mongolian ancestor.

	Male index	Female index
Eastern (Greenland) Eskimo (U.S. N. Museum)	31·00	31·11
Western (St Lawrence Island) Eskimo (U.S. N. Museum)	32·5	33·8
Mongol (U.S. N. Museum)	35·4	36·6

THE AVERAGE $\frac{\text{NASAL WIDTH}}{\text{FACIAL HEIGHT}}$ INDEX IN THE AMERICAN INDIAN

The Arikara Indian crania in Hrdlička's catalogue (5) were those selected to represent the American Indian, as they were found to be the largest single tribal group in that catalogue. The Arikara Indians, it may be noted, were located mainly in South Dakota. The crania that were available for the present research consisted of fifty-one male, from 325362 to 325424, and forty-two female, from 325370 to 325417.

The average index for the males was ascertained to be 34·4, the error of the mean being calculated to be $\pm$ 0·2596. The average index for the female crania was, as in the Mongol and Eskimo racial groups, again slightly higher, namely 35·2. The error of the mean was in this instance $\pm$ 0·2943. The sexual difference was thus nearly three times the amount of the mean error, and therefore possessed a definite degree of significance in this cranial group. It may be further noted that the indices for these Arikara Indian male and female crania, though slightly less than those for the Mongol crania, were still comparable to them, and suggested a certain degree of affinity with the Mongolian type of index, as one would expect.

The writer decided next of all to test the existence of the sexual factor in these American Indian crania by investigating the percentage reductions of the average facial height and the average nasal width in the female as compared with the male crania. As a result he ascertained that the average facial height of the female crania, when compared with that for the males, exhibited a reduction of 5·8 per cent. As a contrast to this, it was found that the amount

of reduction of the average nasal width in the females from that of the males was definitely less, namely 3·5 per cent. Thus, just as in the case of the Mongol and Eskimo crania, the average nasal width in these female American Indian crania approximated more closely to the average for the males than did the average for their facial height (see Table VI). This circumstance was sufficient to explain the increase in the $\frac{\text{nasal width}}{\text{facial height}}$ index in the females as contrasted with the index for the males.

THE AVERAGE $\frac{\text{NASAL WIDTH}}{\text{FACIAL HEIGHT}}$ INDEX IN THE SCOTTISH CRANIA

The writer decided to utilise Turner's Scottish crania as representative of the European type of skull. He therefore calculated the index from the nasal width and facial height measurements given in Tables I to XV of Turner's memoir (8) on "The Craniology of the People of Scotland." It was found that sixty-seven male and thirty-one female crania yielded the measurements that were necessary for the calculation of the index. The marked disproportion between the numbers of crania representative of the sexes was rather unfortunate, and probably explained why the sexual factor was not very pronounced in this racial group.

The average index for the males was 32·36, with a mean error that was calculated to be ± 0·2348. As in the case of all the racial groups that have been previously studied, the average index for the female crania was slightly higher, namely 32·91. The error of the mean in this instance was calculated to be ± 0·4068. The sexual factor was thus not very strongly displayed, but it will be shown in the next paragraph that other proofs of its existence were forthcoming. It may be noted that the average indices for these Scottish crania were comparable with those for the Eskimo. For instance, they were slightly greater than those for the Eastern Eskimo, but fractionally less than those for the Western Eskimo.

The existence of the sexual factor in these Scottish crania was again tested by studying the percentage reductions of the average facial height and the average nasal width in the female as contrasted with the male crania. It was found that the average facial height of the female crania, when contrasted with that for the males, displayed a reduction of 6·5 per cent. On the other hand, it was ascertained that the amount of reduction of the average nasal width in the females from that for the males was definitely less, namely 4·4 per cent. Thus, just as in the case of all the racial types that have been investigated so far, the average nasal width in these female Scottish crania approximated more closely to the average for the males than did the average for their facial height (see Table VI). This fact sufficed to explain the increase in the $\frac{\text{nasal width}}{\text{facial height}}$ index in the female, as contrasted with the index for the male crania.

THE AVERAGE $\frac{\text{NASAL WIDTH}}{\text{FACIAL HEIGHT}}$ INDEX IN THE AMERICAN NEGRO

The data for calculating the index in this racial group were found in Hrdlička's catalogue (6). The writer utilised only those crania that were marked "full blood" on pages 133, 134, 137 and 138 of the catalogue. As a result, rather small numbers of crania were available, namely twenty-two male and twelve female.

The average index for the male crania was calculated to be 38·1, which represented a marked increase when compared with the average indices for the racial types that have been previously studied in this memoir. This high index was of course due to the increased nasal width, which is such a feature of the skull in the Negro races. The index for these male American Negro crania thus taught us that the nasal width was, on the average, 38·1 per cent. of the facial height, which was certainly an important piece of information. The average index for the females of this group was found to be definitely higher than that for the males, namely 40·1. Therefore it was evident that the sexual factor, which was a feature of all the racial types that have been previously studied in this research, existed also in this Negro group.

The writer decided to investigate this sexual factor further by studying the percentage reduction of the nasal width from male to female, and comparing it with the percentage reduction of the facial height from male to female. Thus it was ascertained that the average facial height of these female Negro crania, when compared with that for the males, exhibited a reduction of 8·7 per cent. As a contrast to this it was found that the degree of reduction of the average nasal width was decidedly less, the actual figure being 3·0 per cent. These results are displayed in Table VI. This pronounced difference provided us of course with a ready confirmation of the existence of the sexual factor in this racial group.

THE AVERAGE $\frac{\text{NASAL WIDTH}}{\text{FACIAL HEIGHT}}$ INDEX IN THE ABORIGINAL AUSTRALIAN

These crania were entered in Hrdlička's catalogue (6) as from the Southern Territory. The fifty male crania were from b 33 on page 4 to 237 on page 5. The fifty female crania were from 2027 on page 40 to T 4 on page 41.

The average index for the males proved to be 38·68. The error of the mean in this case was calculated to be $\pm$ 0·2928. It may be noted that the average index for these male Australian crania was fractionally higher than the average for the American Negro males.

The average index for the female crania proved to be 38·70, that is to say, only fractionally higher than that for the males. Still it should be noted that it followed the results obtained from all the racial types which have been studied so far. The error of the mean for these female Australian crania was calculated to be $\pm$ 0·3415.

Although the sexual factor was almost a negligible quantity in this cranial group, it was decided to give it further study by investigating the percentage reductions of the nasal width and facial height in the female crania. This procedure was carried out in all the racial groups that have been previously studied, and in every case confirmed the existence of the sexual factor. By means of a simple calculation it was noted that the average facial height of these Australian female crania, when compared with that for the males, displayed a reduction of 6·4 per cent. On the other hand, it was ascertained that the degree of reduction of the average nasal width was, as usual, slightly less, the actual figure being 5·3 per cent. These results are shown in Table VI. There could thus be no doubt of the existence of a sexual factor, slight though it was, in this racial group.

THE AVERAGE $\frac{\text{NASAL WIDTH}}{\text{FACIAL HEIGHT}}$ INDEX IN THE ABORIGINAL TASMANIAN

The numbers of crania in Hrdlička's catalogue (6) representative of this most interesting racial type were unfortunately very small, amounting to only fifteen male and fourteen female. It may be stated, however, that the results which were obtained consistently followed those yielded by all the racial types previously studied.

The average index for the male crania proved to be as high as 39·4. That is to say, the index evidently reached its maximum in this racial type, so far as one could ascertain with the material at present at one's disposal. These results, it may be added, were confirmed very decisively by the female crania, the average index for these being as high as 42·0. There could thus be no dubiety regarding the fact that the $\frac{\text{nasal width}}{\text{facial height}}$ index was definitely higher in the Negro races than in all the other races that were studied in connection with this research.

It may also be noted that the sexual factor was likewise definitely displayed by these Tasmanian crania. The high average for the females was certainly most striking. In fact it should be added that in only two of the female crania did the index sink below 40.

The writer decided to investigate the sexual factor a little further by studying the percentage reduction of the facial height and the nasal width in the female crania. He found that the average facial height in the females, when compared with that for the males, exhibited a reduction of 7·4 per cent. As a contrast to this result it was found that the percentage reduction of the nasal width was, as usual, definitely less, being only 2·9 per cent. There could thus be no question regarding the existence of a sexual factor in the case of these Tasmanian crania.

Table V.

The $\frac{\text{nasal width}}{\text{facial height}}$ index was found to be lowest in the Eskimo, and highest in the Negro races. Note also that in every instance the index was higher in the females than in the males.

	Males	Females
Eastern (Greenland) Eskimo (U.S. N. Museum)	31·00	31·11
Canadian Arctic Expedition Eskimo	29·4	31·2
Scottish crania (Turner)	32·36	32·91
Western (St Lawrence Island) Eskimo (U.S. N. Museum)	32·5	33·8
Arikara American Indian (U.S. N. Museum)	34·4	35·2
Mongol (U.S. N. Museum)	35·4	36·6
American Negro (U.S. N. Museum)	38·1	40·1
Australian Aboriginal	38·68	38·70
Tasmanian Aboriginal	39·4	42·0

Table VI.

Note that in nine racial groups the percentage reduction of the average nasal width in the female as compared with the male crania was in every instance definitely less than that of the average facial height.

	Average reduction in nasal width (%)	Average reduction in facial height (%)
Eastern (Greenland) Eskimo (U.S. N. Museum)	6·2	7·1
Canadian Arctic Expedition Eskimo	6·8	8·3
Scottish crania (Turner)	4·4	6·5
Western (St Lawrence Island) Eskimo (U.S. N. Museum)	2·9	8·3
Arikara American Indian (U.S. N. Museum)	3·5	5·8
Mongol (U.S. N. Museum)	6·9	9·9
American Negro (U.S. N. Museum)	3·0	8·7
Australian Aboriginal	5·3	6·4
Tasmanian Aboriginal	2·9	7·4

CONCLUSIONS

1. The $\frac{\text{nasal width}}{\text{facial height}}$ index has never been previously described, so far as the author can ascertain.

2. It is obtained by multiplying the nasal width by one hundred and dividing the result by the nasion-alveolar height.

3. It was studied in nine racial groups, and as a result was found to reach its minimum in the Eskimo and its maximum in the Negro races, culminating in the Tasmanian (see Table V).

4. In all these racial groups, without exception, the index was ascertained to be higher in the females than in the males, thus suggesting the existence of a sexual factor (see Table V).

5. The existence of this sexual factor was also shown by the fact that the percentage reduction of the average nasal width in the female, as contrasted with the male crania, was in every instance less than that of the average facial height (see Table VI).

6. The $\frac{\text{nasal width}}{\text{facial height}}$ index in the Western Eskimo represents the transition stage between the index of the Eastern Eskimo and the index of his Mongolian ancestor.

7. The author is becoming more and more confirmed in his opinion that Craniometry can never be made a real Science until the influence of the sex-factor becomes fully accepted. In all craniometric work the male and female crania should be rigorously segregated.

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THE POSITION OF THE EXTERNAL AUDITORY MEATUS

By Prof. F. G. PARSONS
University of London

In contrasting the auricular height of living heads with that of skulls the anthropologist is faced with the want of knowledge of what relation the opening of the living meatus bears to the bony orifice in the skull. Naturally he turns to the anatomist for help and the latter is finding the answer a very difficult one.

It seemed to me that a series of coronal sections through the external and internal auditory meatus of the undissected head would at least give some

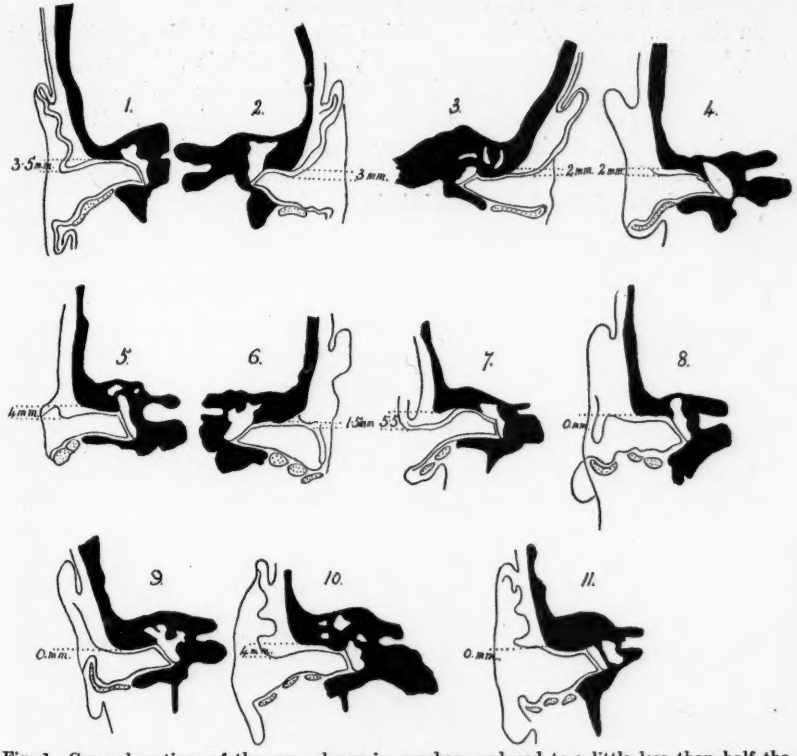

Fig. 1. Coronal sections of the ear—eleven in number—reduced to a little less than half the natural size. The bony parts are black and the actual height of the bony external meatus above that of the soft parts is given in mm.

idea of the amount of variation to be expected, and, as a contribution to our knowledge, I am able to record tracings of sections of eleven ears. It will be seen from these that the bony meatus usually, though not always, is higher than the skin orifice, if we agree to take the lower margin of the crus helicis as the upper limit of the opening; and that the difference between the two varies from nothing to 5·5 mm., with an average of 2·3 mm.

I am glad to hear that other workers are making observations by other methods, and their results will be very welcome since the matter is so important.

In my presidential address to Section H of the British Association in 1927 I allowed only 1·5 mm. for the difference between the bony and cutaneous orifices and I still think that I was not far out, for I took the height of the living head with a Gray's auricular craniometer, fitted with a ratchet attachment which releases the screw when a certain resistance is reached; but this resistance I noticed did not begin to operate until the cutaneous orifice had been drawn up, often for two or three millimetres.

In the new radial craniometer, which the Anthropological Institute is supplying, the ratchet has been abandoned, and I think it will be well if we all agree to use no pressure or traction at all, but to cease screwing so soon as the person being measured feels the instrument touching his skin. If this plan is adopted we may, I think, until further observations are forthcoming, take 2·3 mm. as a fair addition to the skull height to allow for the auditory meatus being lower in the living head than it is in the skull.

THE THICKNESS OF THE LIVING SCALP

By Prof. F. G. PARSONS
University of London

In comparing living heads with skulls it is just as important to know what allowance should be made for the thickness of the scalp as it is to have a just knowledge of the position of the external auditory meatus.

A good deal of work has been done by different anatomists on the thickness of the dead scalp and the general opinion now, I think, is that 4 mm. is a fair working allowance to make.

I have convinced myself in the post-mortem room, by sticking a needle into the scalp and measuring the amount which had penetrated the soft parts, that this allowance is about the average, but lately it has been suggested, quite reasonably, that during life the tissues are probably thicker than they are after death.

To meet this difficulty a needle was devised by Mr Wm Finerty of the Royal College of Surgeons, London. He has fitted it with a vernier scale, and hopes that it may be used on the living head, since the pain would be very trifling; but, unfortunately, the risk of septic trouble following the punctures seems greater than either he or I thought, and I find it impossible to get the permission of the Hospital authorities to use the instrument either upon patients or students even if they voluntarily submit to it. I have therefore had to think of other methods and believe that a good deal may be learned from radiograms.

Dr Fildes, the radiologist at St Thomas's Hospital, has been kind enough to take radiograms of the heads of five students in such a way that the scalp shows quite distinctly, but the difficulty is to estimate the amount of magnification which has taken place. It seems to me, however, that this may be done by taking the length of the head, including the soft parts, in the radiogram, and then the length of the living head with the calipers. In this way the proportion of the actual head length to that of the radiogram may be learned. and the same proportion should apply to the scalp.

The tracings show the contours of the radiograms of the five students, reduced to quarter scale, and the numbers indicate the thickness of the radiogram of the scalp in various places. Accompanying each is the rule of three sum by which the amount of magnification of the thickness of the scalp is found.

It represents in each case

$$\frac{\text{Actual head length} \times \text{radio thickness of scalp}}{\text{Radio head length}} = \text{Actual thickness of scalp.}$$

The result is an average thickness of 5·7 for the living scalp, a perfectly reasonable result if we are right in taking 4 mm. as the thickness of the dead

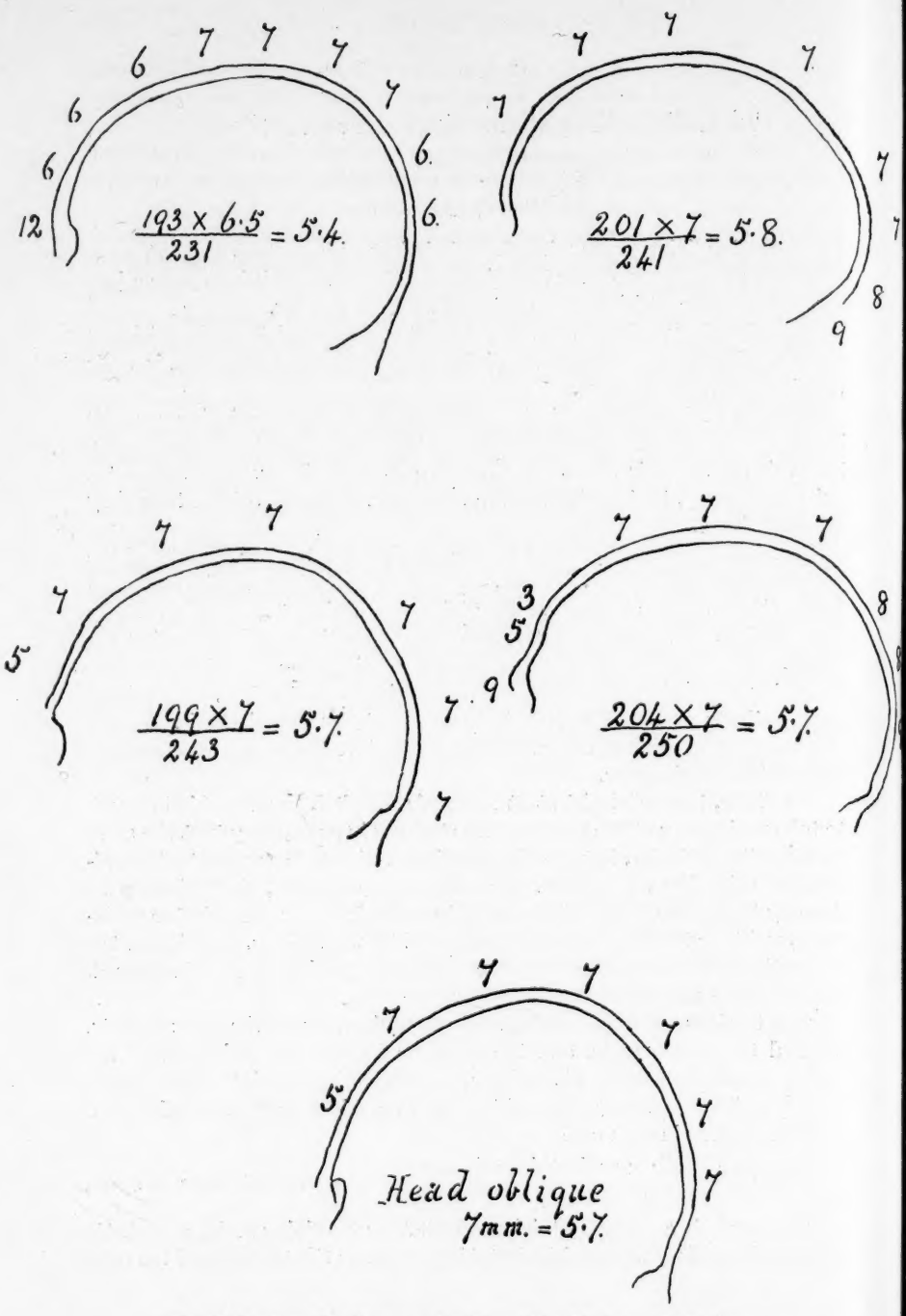

Fig. 1. Tracings of radiograms of scalp mentioned in text. ½ nat. size.

scalp. I must, however, point out that the outer limit of the radiogram of the scalp shows a zone of haze which I have ignored in my measurements, though I am unable to understand to what it is due.

I would suggest that, in comparing living heads with skulls, in the future, it will be well to allow 5·7 mm. instead of 4 mm. for the thickness of the living scalp, except in the forehead, where 4 mm. is ample.

To me the interest of this communication, as well as that upon the "External Auditory Meatus," which precedes it, is the difference which it makes in the proportional indices of skulls when we are comparing them with living heads, and how far it modifies my contention that the heads of Englishmen of this generation are proportionately higher than those of one to two hundred years ago. With the object of testing this I have made the new allowance for soft parts in the collection of eighteenth-century skulls found under the foundations of the old King's College Hospital, often referred to as the Clare Market skulls.

The average length of these skulls was 188 mm., and to this I now propose to add 4 mm. for the soft parts of the forehead, and 5·7 mm. for the scalp in the occipital region; giving a total living length of 197·7 mm.

The average skull breadth was 142 mm., to which 5·7 + 5·7 must be added for the soft parts on each side, making 153·4 mm.; while to the auricular height of the skull, from the top of the auditory meatus, viz. 114 mm., 5·7 mm. must be added for the thickness of the living scalp on the top of the head, and 2·3 mm. for the higher position of the bony external auditory meatus, thus making the living auricular height 122 mm.

The sum of these three diameters is 473·1 and the proportional indices will be

$$\text{Length } \frac{197{\cdot}7}{473{\cdot}1} = {\cdot}418. \quad \text{Breadth } \frac{153{\cdot}4}{473{\cdot}1} = {\cdot}324. \quad \text{Height } \frac{122{\cdot}0}{473{\cdot}1} = {\cdot}258.$$

When these are compared with the former allowance which I made in my address on "The Englishman of the future," read to Section H of the British Association in 1927, it will be seen that the proportional indices at which I then arrived were L. ·421, Br. ·322, Au. H. ·257, giving a difference of only ·001 in the height, which is hardly worth noticing.

To those who have not seen the list referred to I may point out that the proportional height of the heads of hospital patients to-day is ·271, of hospital students ·272, while that of the staff of University College reaches ·278.

FUNCTION OF THE CARTILAGES OF SANTORINI

By V. E. NEGUS, M.S., F.R.C.S.

The arytenoid cartilage in man is continued backwards towards the mouth of the oesophagus in the form of a hook-like process known as the cartilage of Santorini; the only demarcation between the body of the main cartilage and its backward projection is a histological difference (fig. 1).

To discover the function of the process it is necessary to examine the larynx of various animals, in many of which it is of greater importance, both as regards function and size.

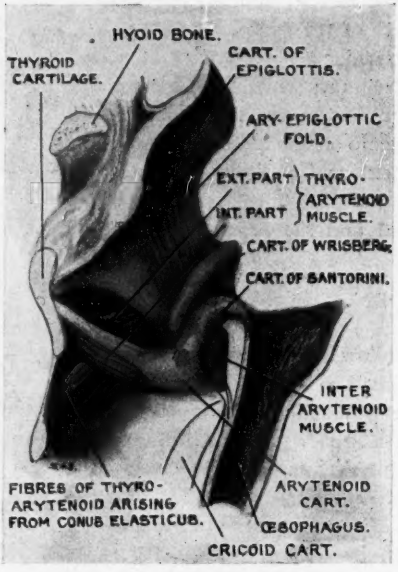

Fig. 1. Left half of larynx of a man aged 50, dissected to show the cartilages of Wrisberg and Santorini (*Homo sapiens*).

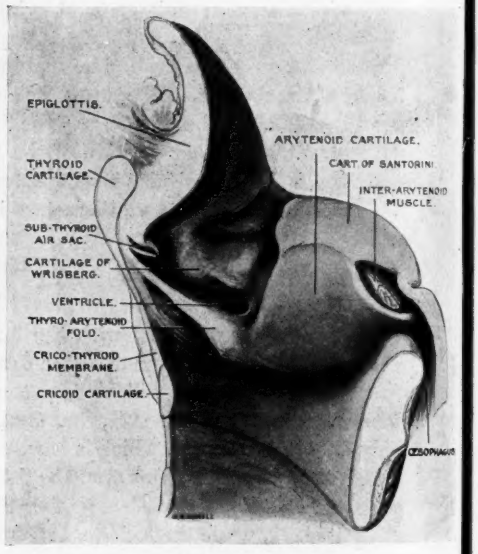

Fig. 2. Left half of dissected larynx of a horse (*Equus caballus*).

The horse (*Equus caballus*) may be taken as a good example (fig. 2). If its larynx be dissected it will be found that the ventral wall of the oesophagus has no attachment to the cricoid cartilage, but is readily lifted away from the back of the larynx. On following the wall upwards it is seen to terminate at the tip of the cartilage of Santorini, from which it is in fact suspended.

Below the curving process lies the inter-arytenoid muscle, resting partly against the process itself and partly against the body of the arytenoid cartilage.

On examining the larynx of a kangaroo (*Macropus giganteus*) the cartilages are seen to curve backwards as long hooks, but a slight modification is found, in that the part of the inter-arytenoid muscle in contact with them is replaced by a sesamoid cartilage (fig. 3). The object of this is to reduce friction when the muscle contracts in closing the larynx in conjunction with the rest of the sphincteric girdle. The arytenoid cartilage is drawn forwards towards the cushion of the epiglottis and the lateral margins of the laryngeal aperture are pressed together, preparatory to the passage of food or drink.

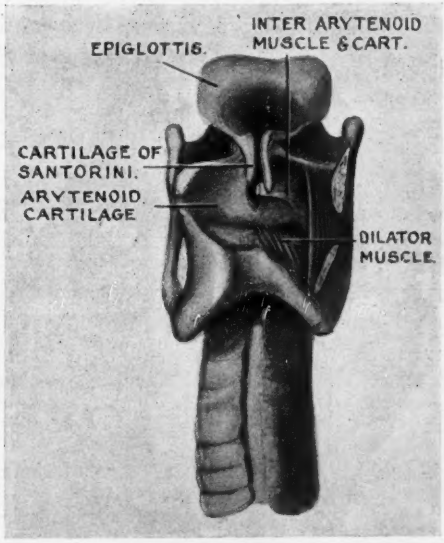

Fig. 3. Dissected larynx of a kangaroo (*Macropus giganteus*) seen from dorsal aspect. (Illustrated in *Journal of Laryngology and Otology*, Nov. 1925.)

When the inter-arytenoid muscle presses the arytenoid cartilage forwards, it causes it to tilt owing to the position of the crico-arytenoid joint; in this tilting movement the cartilage of Santorini takes part as it rotates round the arc of a circle in such a way that its tip moves upwards and forwards in a cephalic and ventral direction.

As the ventral oesophageal wall is attached to the tips of the processes, it is pulled in the same direction and the mouth of the gullet is opened in a funnel-like manner at the moment when the larynx closes.

The crico-pharyngeus muscle relaxes and the bolus of food finds a free passage from pharynx to oesophagus.

In a fox-terrier dog (*Canis familiaris*) a still further modification may be observed, namely that some fibres of the thyro-arytenoid muscle of each side are continuous with longitudinal fibres of the oesophagus (fig. 4).

In this animal the oesophagus will not only be drawn open but it will—by the contraction of these muscle fibres—help to open itself, and to draw its walls over the descending bolus of food. As the latter is prevented from retreating and is pressed onwards by contraction of the inferior constrictor muscle there will be brought into play a creeping movement of the oesophagus over the bolus, much in the manner in which a snake engulfs its prey.

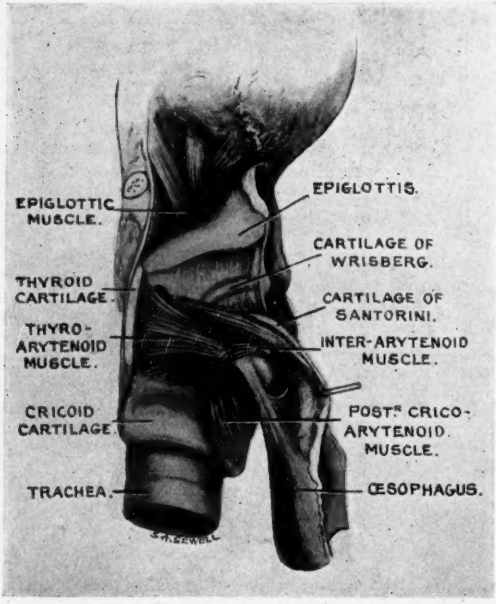

Fig. 4. Dissected larynx of a fox-terrier dog (*Canis familiaris*), showing the continuity of thyro-arytenoid muscle with longitudinal fibres of the oesophagus. (Illustrated in *Journal of Anatomy*, Oct. 1927.)

On examining the arytenoid cartilage of other animals, no process comparable to that of Santorini is found in Amphibians, Reptiles or Birds, in all of which a small larynx lies flat in a capacious pharynx. In none of these animals does the larynx offer any impediment to the onward passage of food, nor is there any sudden narrowing between pharynx and oesophagus as in Mammals. Most Cetaceans do not need to close the larynx during deglutition and in them no cartilage of Santorini is present.

Marsupials have the process well developed, but members of the cat tribe

are poorly provided for; their larynx is of a simple type and does not show the higher modification in any degree of elaboration.

Rodents have but a small cartilage but most Ungulates possess a well-marked one; the pig tribe shows a very long and slender process. The dog tribe has a very long process and there is slight attachment of the oesophagus to the back of the cricoid plate, a feature seen to a greater degree in man.

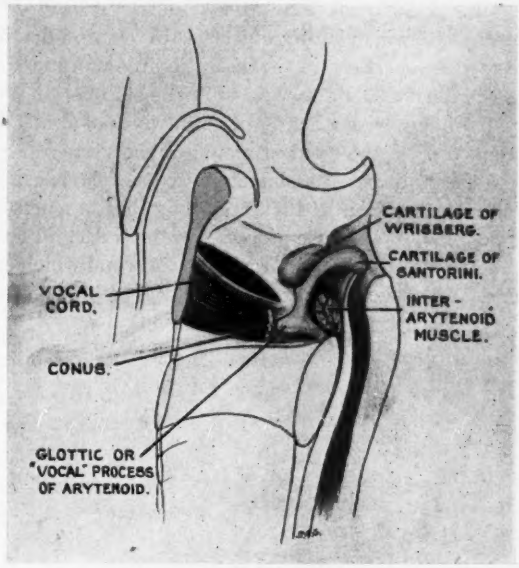

Fig. 5. High cartilages of Santorini in a sooty mangabey monkey (*Cercocebus fuliginosus*).

Most of the monkey tribe have a very long hooked cartilage with almost complete suspension of the oesophagus, as well illustrated in a sooty mangabey monkey (*Cercocebus fuliginosus*) (fig. 5); in man the suspension is less complete, but still is quite obvious if looked for.

To summarise: the cartilage of Santorini is present to give attachment to the ventral wall of the oesophagus and to assist in a mechanism by which the mouth of the oesophagus is opened during deglutition.

AN EXAMPLE OF THE CERVICO-COSTO-HUMERAL MUSCLE OF GRUBER

By A. B. APPLETON and P. H. R. GHEY
Anatomy School, Cambridge University

The anomalous muscle which is the subject of this communication was found on the left side of a female body, in the dissecting room of human anatomy in the Cambridge University Anatomy School in the summer of 1928.

A long muscular band, with a nearly uniform width of about three-quarters of an inch, extended from the cervical region of the vertebral column to the surgical neck of the humerus, passing deep to the clavicle and below the coracoid process of the scapula. It took origin, by short aponeuroses, from the posterior tubercles of the transverse processes of the sixth and seventh cervical vertebrae. In addition, it took origin from a fascial band which extended from the seventh cervical transverse process to the fascia of Sibson.

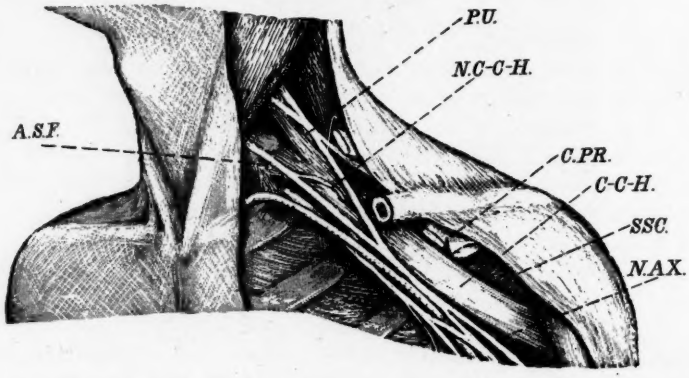

Fig. 1. Diagram of dissection of the neck and axilla to show the attachments, relations and nerve-supply of M. cervico-costo-humeralis. *C-C-H.* Cervico-costo-humeral muscle. *N.C-C-H.* Nerve to the cervico-costo-humeral muscle from the anterior division of the middle trunk of the brachial plexus. *P.U.* Posterior division of the upper trunk of the brachial plexus. *A.S.F.* Attachment of the cervico-costo-humeral muscle to Sibson's fascia; adjacent to it are shown the attachments of the muscle to the sixth and seventh cervical transverse processes. *N.AX.* Axillary nerve. *C.PR.* Coracoid process with attachments of Mm. pectoralis minor and coraco-brachialis (cut). *SSC.* Subscapularis muscle.

The muscle had a linear aponeurotic insertion on the surgical neck of the humerus immediately distal to the lesser tubercle and separated by a small interval from M. teres major.

Apart from the short aponeurotic portions adjacent to the attachments, the structure was muscular in its whole length.

The nerve-supply was derived from the seventh cervical nerve through a small branch of the anterior division of the middle trunk of the brachial plexus. This nerve entered the superficial surface of the muscle in the subclavian triangle of the neck (fig. 1).

OTHER RELATIONS

At its origin the muscle was situated between Mm. scalenus anterior and scalenus medius. Close to its origin it was placed between the upper and middle trunks of the brachial plexus. More laterally, the muscle passed behind the anterior division and in front of the posterior division of the upper trunk of the plexus. The muscle was situated in the subclavian triangle of the neck a little below the omohyoid muscle and above the lateral cord of the plexus. In the axilla it was closely applied to the axillary surface of M. subscapularis, and was above the axillary vessels and deep to the costo-coracoid membrane and Mm. subclavius and pectoralis minor. Close to its insertion it crossed the upper part of the quadrangular space, and the axillary nerve passed below its inferior margin.

PREVIOUSLY-RECORDED EXAMPLES

This muscle must be one of extreme rarity, in view of the small number of recorded instances. Only four such instances are known to us, viz. those of Gruber (1857), Ransom (1885), Weber et Collin (1905) and Loth (1917). In none of these cases was any statement provided as to the nerve-supply of the muscle; but the descriptions justify their being classified together. Ransom employed the term "cervico-humeral" and Loth used the name "cervico-capsulo-humeralis"; but Gruber's name of "cervico-costo-humeralis" has the claim of priority. The term "cervico-humeral" was employed by Humphry, moreover, to describe a muscle (the "omocervicalis" of Bischoff and Eisler) which requires to be carefully distinguished from Gruber's M. cervico-costo-humeralis. The difference between these muscles will be discussed in another contribution to the present number of this *Journal* (p. 437).

Loth has drawn attention to the difficulty of finding Gruber's description of his example of this anomalous muscle. The reference which is provided by most authors is inaccurate. Gruber's communication is dated 1857, and was published in the *Mémoires présentés à l'Académie Impériale des Sciences de St.-Pétersbourg par Divers Savants*, tome VIII, 1859. The account is to be found on pp. 249 and 250. An outline copy of the drawing provided by Gruber (Taf. 4, fig. 2) is furnished in a separate contribution by one of us (A. B. A.) to the present number of this *Journal* (p. 441).

The vertebral attachment of the muscle was restricted to the seventh cervical vertebra in the examples of Ransom and of Weber and Collin, that of Gruber was restricted to the sixth vertebra, while in Loth's, as in ours, the

muscle was attached to both the sixth and the seventh cervical vertebrae. Gruber's example had also a tendinous origin from the ventral end of the first rib.

The insertion of the muscle was blended with that of M. subscapularis on the lesser tubercle of the humerus in the cases of Ransom, and of Weber and Collin. In Gruber's example the insertion was similar to that of our case, viz. on the medial side of the surgical neck of the humerus. Loth's example (for the reference to which we are indebted to Dr W. L. H. Duckworth) offers an interesting variant of the mode of insertion of the muscle. The principal insertion was some centimetres distal to that of M. latissimus dorsi. An additional insertion was provided by a small muscle-slip which gained attachment to the capsule of the shoulder-joint. Finally, a small muscle-belly arose from the under surface of this joint capsule; it joined the main tendon of the muscle and then attached itself to the tendon of insertion of M. latissimus dorsi.

In all the above-cited instances of the cervico-costo-humeralis muscle the relations were clearly similar to those which we found in our example. In all cases except that of Ransom it is stated that the anomalous muscle was unilateral.

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ON THE MORPHOLOGY OF THE CERVICO-COSTO-HUMERALIS MUSCLE OF GRUBER

By A. B. APPLETON

Lecturer in Anatomy, Cambridge University

An example of this muscle has been described in the present number of this *Journal* (p. 434 and fig. 1), with references to the few other recorded instances of its occurrence. It extended from the sixth and seventh cervical vertebrae to the surgical neck of the humerus, and it appears to be the only example in which the nerve-supply has been placed on record. This was derived from the seventh cervical nerve, through the anterior division of the middle trunk of the cervical plexus. M. cervico-costo-humeralis has been described only in man. It is, indeed, somewhat remarkable that there is not (so far as I can ascertain) any record of the occurrence in other Mammals of a muscle which can be homologised with M. cervico-costo-humeralis, provided that due attention is given to attachments, relations and nerve-supply.

DISTINCTION OF M. CERVICO-COSTO-HUMERALIS FROM M. OMOCERVICALIS (*SEU* LEVATOR CLAVICULAE)

Various writers have homologised the cervico-costo-humeral muscle with M. omocervicalis (Bischoff, 1870), a muscle which has a wide distribution among Mammals and has been involved in adaptations of the shoulder-region to a cursorial habit of life in various Mammalian orders.

Le Double, in his *Traité des variations du système musculaire de l'homme* (1897), claimed the presence of a cervico-costo-humeral muscle in a number of animals, citing the rabbit, hedgehog and guinea-pig as presenting well-developed examples. Testut (1884), referring to Sabatier, compared the cervico-costo-humeral muscle with the masto-humeral and acromio-transverse muscles of non-claviculate Mammals, and claimed that it offers an exact reproduction of one of the lower fascicles of the masto-humeral of the dromedary ("devenu un trachelo-huméral"). But these muscles are specialised derivatives of Mm. omocervicalis and cleido-mastoideus.

Now if we employ the term "omocervicalis" in the same way as Eisler (1912, p. 243), the muscle so designated differs from M. cervico-costo-humeralis in its attachments, in its relations and in its nerve-supply.

Nerve-supply. The omocervicalis is known to be innervated in a number of Mammals from the cervical plexus (Eisler). This muscle is occasionally present also in man (sometimes described as "levator claviculae"), and it has been found to receive its nerve-supply from the third cervical nerve (Eisler, 1912,

p. 245), in close association with the nerves to M. trapezius from the cervical plexus. The innervation of M. cervico-costo-humeralis was, on the other hand, derived from the middle trunk of the brachial plexus in the one instance in which the innervation has been recorded.

Attachments. In its proximal attachments the omocervicalis presents some resemblance to the cervico-costo-humeralis muscle; it is, however, in most Mammals (e.g. in *Hapale* as the so-called "levator scapulae anticus" of Beattie) attached to more cranial vertebrae than the cervico-costo-humeralis, which arises from the sixth or seventh cervical vertebra.

But in its distal attachments the omocervicalis presents a striking contrast to the cervico-costo-humeral muscle. The omocervicalis, in its presumed primitive form, is attached to the acromion of the scapula and to the adjacent part of the clavicle. It is only in certain Mammals that it has any attachment to the humerus; and it can scarcely be doubted that they are examples of specialisation.

The omocervicalis has gained an attachment to the humerus in at least two ways in Mammals. In rare instances the insertion of the muscle has extended beyond the acromion to the fascia superficial to the greater tubercle of the humerus (*Erethizon*) or to the fascia over M. teres minor (*Hyrax*); or it may gain a direct attachment through fascia to the greater tubercle of the humerus (*Phoca*). This method of attachment to the humerus differs completely from that of M. cervico-costo-humeralis.

Another modification of the shoulder-region which involves an indirect attachment of M. omocervicalis to the humerus consists in the reduction of the clavicle to a vestige, sometimes represented by no more than a tendinous intersection separating neck from arm musculature. It is thus that in various cursorial Mammals the omocervicalis comes to form the cervical part of a single mechanical unit, the distal part of which consists of an arm muscle, e.g. a part of the deltoid. The compound muscle thus formed extends from the skull or vertebral column to the humerus, and presents an intersection or vestigial clavicle at the boundary between the zones innervated respectively from the cervical plexus and a metazonal branch of the brachial plexus (e.g. the axillary nerve, as in the rabbit). It has been variously described as "mastohumeralis," "basiohumeralis," "cephalohumeralis," or "brachiocephalicus."

Now a structural modification of this character can be excluded from the history of the Primates; and the cervico-costo-humeral muscle shows in the manner of its innervation no resemblance to the diploneural brachiocephalicus.

Relations. Those varieties of M. omocervicalis which have an attachment to the humerus differ considerably from M. cervico-costo-humeralis in their relations. When a direct attachment to the humerus is present (e.g. in *Phoca*) the omocervicalis approaches the humerus by passing over the cranial aspect of the shoulder-girdle; but the cervico-costo-humeralis passes to the caudal side of the clavicle and coracoid process.

When, on the other hand, the attachment of M. omocervicalis to the humerus is attained through the formation of a compound brachiocephalicus, the vestige of the clavicle is embedded in the muscle, and the muscle passes to the cranial side of the coracoid process when this is present as a well-developed structure. The relations of this brachiocephalicus to the clavicle and coracoid process thus differ in important respects from those of the cervico-costo-humeral muscle.

It is concluded, then, that the omocervicalis muscle differs in its attachments, relations and nerve-supply from the occasional M. cervico-costo-humeralis of man.

It is not improbable that the acceptance by the majority of writers of the view which regards the cervico-costo-humeral muscle as a variant of M. omocervicalis is partly attributable to the similarity of its name to that used for Bischoff's omocervicalis by Humphry (1872, p. 135), viz. "cervico-humeral." Ransom, indeed, employed the latter name in his description of an example of the cervico-costo-humeral muscle of Gruber.

OTHER VIEWS OF THE HOMOLOGY OF THE CERVICO-COSTO-HUMERALIS MUSCLE

Eisler distinguished the cervico-costo-humeralis muscle from the omocervicalis (Bischoff). He was inclined to classify the former of these with Mm. coraco-brachiales minores; but in the absence of information as to its nerve-supply, he expressed himself as unable to exclude the participation of omohyoid musculature in its formation (1912, p. 311).

Certain anomalous human muscles belonging to the omohyoid musculature occupy situations similar to that of the cervical part of M. cervico-costo-humeralis. Sometimes an omohyoid muscle is attached partially or solely to the coracoid process (M. coraco-hyoideus, Hyrtl). Probably to this category belongs also the M. coraco-cervicalis of Krause. Among the muscles of the omohyoid group mention may be made of the cleido-hyoideus (occurring as an anomaly also in the chimpanzee, Gratiolet) and the cleido-fascialis. There is some approximation between the position of anomalous forms of the omohyoid musculature (especially of the coraco-hyoideus) and that of the cervical portion of M. cervico-costo-humeralis. Even a vertebral attachment for M. omohyoid has been recorded (Hallett), though this has apparently not been observed in association with a lateral attachment to the coracoid process.

Comparison of omohyoid musculature with the cervico-costo-humeralis requires, however, that we should offer some account of the distal attachment of the latter to the humerus. The site of this distal attachment is very similar to that of Mm. coraco-brachiales minores (e.g. the "rotator humeri"). It is therefore permissible to enquire whether the cervico-costo-humeralis represents a combination of a proximal omohyoid portion with a distal coraco-brachial portion, with elision of a common attachment to the coracoid process.

This interpretation is, however, excluded by the nerve-supply of the cervico-costo-humeralis. No evidence was found by Appleton and Ghey of a separate nerve-supply for the distal and proximal parts of the muscle. The whole of it received an innervation (p. 435) consistent with allocation of the whole of the muscle to the coraco-brachialis musculature and distinguishing it clearly from the omohyoid musculature.

COMPARISON OF M. CERVICO-COSTO-HUMERALIS WITH MM. CORACO-BRACHIALES

In most of its features the cervico-costo-humeral muscle presents a close resemblance to coraco-brachial musculature. Only in its extension into the neck, and in its attachment to the vertebral column, does this muscle appear to diverge from muscles of the category of the coraco-brachiales minores. The manner of insertion of M. cervico-costo-humeralis, which is on the lesser tubercle of the humerus, on the medial aspect of the surgical neck of the

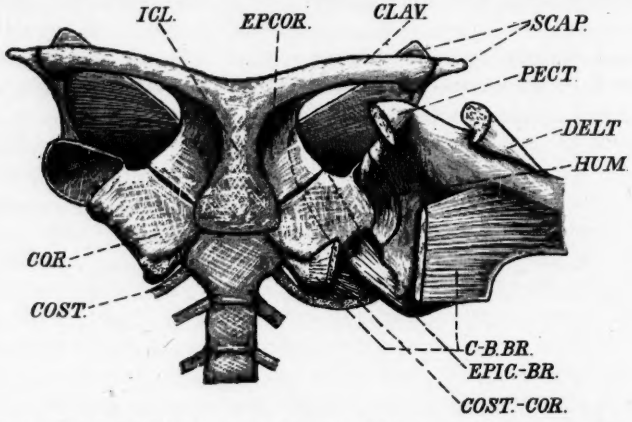

Fig. 1. Pectoral girdle of *Echidna acul.*, with parts of left humerus, sternum and ribs. The left coraco-brachialis brevis muscle is represented as cut, exposing the epicoraco-brachialis and the costo-coracoid muscles. M. epicoraco-brachialis passes cranially, on the dorsal aspect of the coracoid, and is attached to this bone and to the epicoracoid. Parts of Mm. pectoralis and deltoideus adjacent to their humeral attachments are shown. *C-B.BR.* Coraco-brachialis brevis muscle (cut). *EPIC.-BR.* Epicoraco-brachialis muscle. *COST.-COR.* Costo-coracoid muscle, extending from the first rib to the coracoid. *COST.* First rib. *COR.* Coracoid bone. *EPCOR.* Epicoracoid bone. *CLAV.* Clavicle. *SCAP.* Scapula. *PECT.* Pectoralis. *DELT.* Deltoid muscle. *HUM.* Humerus (ventral aspect). *ICL.* Interclavicle.

humerus, or on the capsule of the shoulder-joint, is indistinguishable from that of the coraco-brachialis breves (*seu* minores) which are widespread in Mammals and exemplified in the occasional human "rotator humeri." The relations of M. cervico-costo-humeralis (apart from those involved in its attachment to the vertebral column) are again like those of Mm. coraco-brachiales breves. Now in Monotremata the coraco-brachialis musculature extends more proximally

than in other Mammals (fig. 1) and passes cranially to the first rib but caudally to the clavicle and coracoidal part of the shoulder-girdle. The course by which M. cervico-costo-humeralis enters the neck is similar (Appleton and Ghey, 1929, fig. 1). In the axilla the relations of the cervico-costo-humeral muscle are like those of the human "rotator humeri." It is anterior to the upper part of M. subscapularis, and crosses the upper part of the quadrangular space above the axillary nerve.

The nerve-supply, derived as we have seen from the seventh cervical nerve, indicates that the muscle has a metameric value in ontogeny which associates it with the coraco-brachialis musculature (the latter being normally in man innervated from the sixth and seventh cervical nerves).

Loth's example of the cervico-costo-humeralis muscle offers additional resemblances to the coraco-brachialis musculature, not only in certain details of its attachments but also in its connection close to its insertion with a small muscle which extends from the capsule of the shoulder-joint to the tendon of M. latissimus dorsi. This small muscle may be classified as a "capsularis humero-scapularis" (Gruber, 1859, p. 239), and belongs to the category of Mm. coraco-brachiales minores.

The cervico-costo-humeral muscle therefore presents features which lead to the conclusion that it consists of an extension of coraco-brachialis musculature into the root of the neck.

Now this extension is clearly a caenotelic modification inasmuch as a vertebral attachment is a feature neither of the lower nor of the more specialised Tetrapoda.

There is, however, in the lower Tetrapoda, a comparable proximal extension of the coraco-brachialis musculature, towards the mid-ventral line, on the coracoidal part of the girdle. Even in the most primitive of the modern Mammals, the Monotremata, this arrangement is still found.

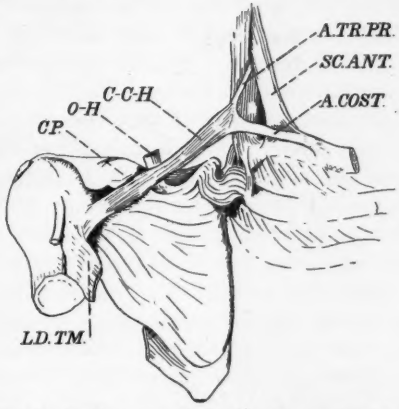

Fig. 2. Outline copy of the drawing provided by Gruber to show M. cervico-costo-humeralis (1859, Taf. 4, fig. 2). *C-C-H.* Cervico-costo-humeral muscle. *A.TR.PR.* Attachment to transverse process of sixth cervical vertebra. *A.COST.* Attachment to ventral end of first rib. *SC.ANT.* Anterior scalene muscle. *CP.* Coracoid process. *LD.TM.* Mm. latissimus dorsi and teres major. *O-H.* Omohyoid muscle.

If, now, it be admitted that a vestigial tendency to the formation of coraco-brachial musculature in the region of the neck may conceivably persist in the therian Mammals (Marsupialia and Eutheria), material support is offered to the interpretation of the cervico-costo-humeral muscle as a cervical extension of the coraco-brachial musculature.

In Monotremata the coraco-brachialis musculature comprises a coraco-brachialis longus inserted distally on the humerus, and two muscles attached on the proximal part of the humerus (fig. 1), the coraco-brachialis brevis and the epicoraco-brachialis. All these have their proximal attachments near the mid-ventral line, on the coracoidal part of the pectoral girdle (viz. on the meta-coracoid and "epicoracoid").

Now Broom and Watson have shown that in certain therian Mammals also we can find evidence of a similar structural pattern in this region of the neck. For in the embryos of certain Marsupialia the cartilaginous coracoid extends from the shoulder-joint across to the sternum and vestigial interclavicle. Subsequently, however, the continuity of this skeletal bar from shoulder to sternum is lost, and the lateral portion is alone retained as a coracoid process on the scapula providing attachment for coraco-brachial and biceps musculature.

While no Eutheria have yet been shown to possess the complete form of the tetrapod coracoid at any period of their life-history, it is nevertheless not improbable, in view of the general anatomical resemblance of Marsupialia and Eutheria, that similar morphogenetic tendencies are present in the latter, though possibly they are never actually realised in the course of development in the formation of a continuous bar of cartilage. This bar has an ephemeral existence in marsupials. The failure in Eutheria of the mesenchyme of this region to develop a recognisable skeletal bar does not necessarily imply any large difference of the potentialities of the embryonic material.

There may well be latent potentialities in the root of the eutherian neck in respect also of musculature, in the region corresponding to the more proximal part of the coraco-brachialis musculature of Monotremata. The opinion is expressed that the occasional development in man of the cervico-costo-humeral muscle provides some evidence that the form-pattern in the root of the neck is still sufficiently like that of primitive Mammals to permit of the occasional realisation of coraco-brachialis musculature in this part of the neck. The proximal extension of coraco-brachialis musculature which appears to have occurred in the formation of the human cervico-costo-humeralis muscle is perhaps not in itself a caenotelic feature; the attachment to the vertebral column, Sibson's fascia or the first rib can alone be so described.

THE VERTEBRAL ATTACHMENT OF M. CERVICO-COSTO-HUMERALIS

While every recorded example of this muscle has presented an attachment to the vertebral column, there has been a more ventral additional attachment in two instances. In Gruber's example there was an attachment to the ventral end of the first rib (fig. 2); in the case described in the present number of this *Journal* (p. 434) there was an attachment to Sibson's fascia.

Now the costal attachment in Gruber's example is in a situation which corresponds closely with the site of attachment of coraco-brachialis muscula-

ture to the pectoral girdle in Monotremata and lower tetrapods. In therian Mammals, on the other hand, the coracoidal part of the girdle (to which the coraco-brachialis musculature is attached in Monotremata) has undergone reduction. In the marsupials it undergoes retrogression early in development, while it never develops as an integral part of the embryonic skeleton in any eutherian Mammal, so far as is known. If, in these circumstances, coraco-brachialis musculature developed in the root of the neck in any eutherian Mammal, it might be expected to gain an attachment to some neighbouring structure such as the ventral end of the first rib or Sibson's fascia (cf. Gruber's example of the cervico-costo-humeral muscle (fig. 2)).

Again, it has been shown that in the young embryo of certain Eutheria there occurs a considerable caudad translation of the pectoral girdle relative to the vertebral column and ribs. Thus it is that the subclavius muscle, extending at first in a cranio-caudal direction from the clavicle to the first rib (man—Lewis, 1910, the albino rat—Blincoe, 1928, fig. 4), comes ultimately to be situated obliquely with the clavicular attachment placed only just cranial to the first rib. If, therefore, the primitive cervical part of the coraco-brachialis musculature developed in a eutherian Mammal such as man, and acquired an early attachment to some neighbouring structure in default of the formation of the primitive Mammalian coracoidal bar, such an attachment would be situated in the region of Sibson's fascia and would not be far distant from the seventh cervical transverse process.

Analogous modifications of muscular attachment have been claimed in respect of various other muscles which are attached to the coracoidal part of the girdle in Monotremata and primitive Tetrapoda. The subclavius is regarded (Eisler) as the therian representative of the costo-coracoid and sterno-coracoid musculature; the origin of M. biceps, along with that of M. coraco-brachialis longus, has been displaced to the lateral end of the coracoidal part of the girdle; while the dorsi-epitrochlearis muscle, attached to the tendon of M. latissimus dorsi or some neighbouring structure, has been interpreted as the representative of the coracoid head of the anconæus (*seu* triceps) of the more primitive Tetrapoda (Eisler).

Thus the proximal attachments of the human cervico-costo-humeralis muscle are not inconsistent with the homologisation of this muscle with a part of the coraco-brachialis musculature of a primitive Mammal. The attachment of M. cervico-costo-humeralis to the vertebral column must, however, still be regarded as a caenotelic feature of man. It may be that this muscle is a variant of the coraco-brachialis musculature with prospective value for human evolution.

A participation of scalene musculature in the definitive attachment of M. cervico-costo-humeralis to the vertebral column cannot be excluded. The primordium of the scalene musculature must be adjacent to the presumed site of development of the cervico-costo-humeral muscle; it may indeed be continuous with the primordium of this muscle. Further, the innervation of the

scalene musculature is derived in part from the same segmental nerve as that of M. cervico-costo-humeralis.

RELATION OF M. CERVICO-COSTO-HUMERALIS TO M. SUBCLAVIUS

The metameric relation of these muscles in man finds a parallel in Monotremata, provided that we accept the view advanced in the preceding pages that the cervico-costo-humeral muscle belongs to the coraco-brachialis musculature, as well as the conclusion of Eisler, that the subclavius muscle is the therian representative of the monotreme sterno-coracoid and costo-coracoid muscles.

The subclavius muscle was formerly thought to have been derived from the pectoral musculature. That this is incorrect appears from the independent appearance of its primordium in the embryo (Lewis), and from the topographical independence of its nerve from the nerves to pectoralis musculature (von Gössnitz, 1901, and Bolk, 1902). In various Eutheria its origin extends to the sternum; and again, in various marsupials and Eutheria, the insertion is on the coracoid process or supraspinatus fascia. Eisler is probably correct (1912, p. 489) in deriving the subclavius muscle from the sterno-coracoid and costo-coracoid musculature of primitive Mammals.

In man the subclavius has the more cranial segmental innervation, viz. from the fifth cervical nerve (with varying contributions from the fourth and sixth); that of the cervico-costo-humeral muscle comes from the seventh nerve.

In Monotremata the nerve-supply of the coraco-brachialis musculature is derived from the musculo-cutaneous nerve. According to the description and figure of McKay (1894) this nerve perhaps includes fibres from the sixth and seventh cervical nerves. The long nerve with an independent course which supplies the costo-coracoid and sterno-coracoid muscles is, on the other hand, derived from a more cranial part of the plexus.

The similarity of the metameric relationship of the supposed homologous muscles in man lends support to the views which have been expressed as to these homologies.

It is probable that the primordia of the subclavius and the cervico-costo-humeralis muscles are in close proximity in the young embryo, before the caudad displacement of the pectoral girdle (to which allusion has already been made) carries the subclavius muscle away from the cervico-costo-humeralis.

The sterno-coracoid and epicoraco-brachialis muscles of Monotremata are in close relationship even in the adult. Despite this close topographical relationship it appears improbable that they represent differentiated portions of a single muscle-mass if we accept Eisler's view regarding the history of the subclavius muscle. Study of the reptiles and Amphibia shows that the sterno-coracoid and costo-coracoid musculature has had a long phylogenetic history independent of the coraco-brachialis musculature. The latter was doubtless

derived from the depressor-abductor ventral musculature of the fish-fin during the evolution of the Tetrapoda; from its very beginning it has been a muscle-mass extending from the ventral part of the primary shoulder-girdle into the limb.

The sterno-coracoid and costo-coracoid muscles have, on the other hand, had a very different history. They appear to have been derived from the segmented body-wall musculature (Miner, 1925, p. 210), where the sternum and interclavicle intrude upon and partially interrupt it. The sterno-coracoid may be regarded as corresponding to the hindmost part of the urodele sterno-hyoid muscle (Miner), while the costo-coracoid is serially homologous with the intercostal musculature. Among modern animals it is only in the Sauropsida and Monotremata that we find them present as definite muscles (unless we include also the therian subclavius).

SUMMARY

The cervico-costo-humeral muscle belongs to the coraco-brachialis musculature.

It is innervated from the seventh cervical nerve.

Its attachment to the vertebral column constitutes a caenotelic feature. The cervical portion of the muscle may represent that part of the coraco-brachialis musculature which in Monotremata and the lower Tetrapoda extends medially to gain an attachment on the primary girdle near the mid-ventral line.

Modification of the coracoidal part of the girdle in therian Mammals has involved the suppression of the more medial part of the coraco-brachialis musculature. But the occasional development in man of a M. cervico-costo-humeralis is perhaps illustrative of a persistent tendency to the development of a form-pattern in the root of the neck similar to that of primitive Mammals, a tendency which is displayed also in the temporary formation of a complete coracoidal bar in the embryos of certain marsupials.

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THE SKULL OF *ORNITHORHYNCHUS*, ITS LATER DEVELOPMENT AND ADULT FEATURES

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and H. C. FURST, B.Sc.

The following description of the *Platypus* skull was inspired by, and is very largely based upon, a very fine series of young skulls placed at our disposal by Prof. Launcelot Harrison, and we have to thank him very sincerely for having given us this opportunity. We have also to thank Dr C. Anderson, the Director of the Australian Museum, for the loan of two adult skulls.

Actually we have had for study nine heads and skulls, of which the first five are those given us by Prof. Harrison.

A brief description of the collection follows.

Specimen A. This was the head taken from a foetus measuring 175 mm. from tip of snout to tip of tail. It should be noted in passing that this specimen was intermediate in age between Prof. Wilson's two foetuses studied by Watson. The skull of this specimen was dissected out and divided along the mid-sagittal plane, one half was dried and the other rendered transparent.

The prepared skull measured 25 mm. from tip of snout to the plane of the occipital condyles.

Specimen B. A dried skull measuring 48 mm. in length. This tiny little skull was completely disarticulated except for the group of bones depicted in fig. 1, p. 449.

Specimen C. A skull 50 mm. in length. In this only sufficient bones have been removed to expose the cranial cavity and the nasal cavity on one side. As would be anticipated there is practically no difference between the bones of these last two specimens, so that we have been able to use the disarticulated specimen to check off form and relations in this skull. There are retained in position in this specimen certain sheets of cartilage and connective tissue which will be described in connection with those bones which our material indicates are developed from them.

Specimen D. 65 mm. in length. In this young skull ossification is so far advanced that all the bones present nearly adult features. All the sutures are open except that between the hinder end of the pterygoid bone and the inner face of the processus alaris, which indeed is closed in Skull *B.* This skull is illustrated in three aspects on Plate I.

Specimen E. 80 mm. in length. This is the young adult skull briefly described by Watson (1916). The full adult condition is reached in nearly all the bones; most of the sutures, though closed, are clearly discernible.

Specimen F. An adult skull 102 mm. long.

Specimen G. A partly prepared skull measuring 112 mm. from tip of cartilaginous snout to occiput. This is apparently a little younger than the last. Both these last two were loaned to us by Dr Anderson.

Specimen H. Over 100 mm. in length, it is the skull of an old adult and was cut about and opened up very completely before it was thought to measure it.

Specimen J. An adult head in the flesh. It was divided along its length just to one side of the mid-sagittal plane. One half was then dissected clean, and both halves were decalcified. The other half was now cut by hand into thick slices and both halves were then rendered transparent. These transparent preparations enabled us to check the course of nerves and vessels, and the position of the cavities of the otic labyrinth.

The last two specimens are the property of the senior author.

A comparison of our 48 and 50 mm. skulls with Prof. Wilson's older foetus, as described by Watson, indicates that there has not been much advance in ossification in the intervening stages. We have therefore a very complete series by which to connect the earlier development of the skull with the adult features.

Particular attention has been paid to this aspect of the work and, as a result, we have been able to correct one or two misinterpretations of the adult skull, notably the origin, extent and situation of the presphenoid and ethmoid ossifications and the discovery that the squamosal bone is excluded from sharing in the formation of the inner wall of the cranial cavity.

We believe that an independent lachrymal bone is present as an independent entity in the youngest skull (25 mm.) and is still recognisable in the 48, 50 and 65 mm. skulls, but on this point we are not able to make a definite statement.

As there is no complete description of the *Ornithorhynchus* skull in the English literature we have extended our work to fill this want.

A discussion on the significance of the alisphenoid lamina of the periotic bone, for which the senior author alone is responsible, forms the concluding portion of this communication.

REGIO OCCIPITALIS

The occipital segment is composed of four separate ossifications.

The *Basioccipital bone* viewed from the ventral aspect in the young adult skull *E* is seen forming the postero-medial part of the basis cranii, and for descriptive purposes it may be said to consist of an anterior and a posterior portion separated, or joined, by a neck which is formed by the encroachment of the two jugular foramina. The anterior portion forms a straight transverse suture with the basisphenoid bone. In the adult skull this suture is bridged in the mid-line by a posterior prolongation of the vomer. Laterally the anterior portion of the bone forms sutures, which diverge posteriorly, with the petrosal bone. The posterior portion of the basioccipital is a stout curved bar of bone

with the concavity of the curve open at the foramen magnum. On either side this bar forms a short straight suture with the exoccipital.

In the 48 and 50 mm. skulls the basioccipital bone is isosceles triangular in outline, but with all three angles truncated. The truncated apex of the triangle is anterior and sutures with the basisphenoid. The straight suture line with the periotic bone commences in front at the side of this truncated apex and extends backward and outward to the jugular foramen. In these young skulls this foramen does not constrict the bone appreciably, and it is of interest to note that in the older skulls, measuring 65 and 80 mm., the basioccipital is actually narrower here than in the younger skulls. One cannot therefore, in the younger skulls, describe the bone as being composed of anterior and posterior portions. The truncated lateral corners provide the face for suture with the exoccipital bones (fig. 1).

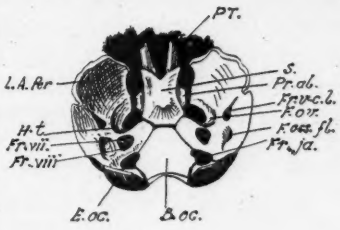

Fig. 1.

In all four mature skulls the basioccipital bone is fenestrated on either side of the mid-line immediately behind the basioccipito-basisphenoid suture. In Skull *F* there are two fenestrae on the left side and two semi-transparent areas of the bone in corresponding situations on the right. The anterior of the fenestrae is situated actually in the line of the suture, and has resulted as much, or nearly as much, from the absorption of the hinder end of the basisphenoid as from absorption of the front of the basioccipital. In Skull *G* the fenestrae are symmetrical and, besides having coalesced on each side, have been extended forward through the basisphenoid to the hinder edge of the carotid foramina. In Skull *H* they have not been run together but the anterior pair extend forward right to the carotid foramina, which in consequence have to be sought on the upper surface of the basisphenoid, where they are found tunnelling forward through the dorsum sella.

The *Exoccipital bones* are irregularly quadrilateral in shape. Each presents an inferior border, much thickened to form the occipital condyle. Situated almost in the coronal plane, the condyles diverge from the sagittal plane at an angle of approximately 45°, the outer ends being the higher. Above the outer end of the condyle the lateral border of the bone forms a straight, nearly vertical suture with the mastoid region of the petrosal bone. The superior border forms another straight suture, with the horizontal lower border of the supraoccipital bone.

The *Supraoccipital bone* is roughly half-moon shaped, with its long axis transverse. It covers, in the posterior portion of the cranial cavity above, the foramen magnum across nearly the whole width of the skull. Dorsal and lateral margins merge in one full sweep, though the parietal border is slightly straightened out, forming a transverse suture with the posterior border of the

parietal bone. The inferior margin sutures with the exoccipital on each side, and lateral to this with the parietal lamina of the petrosal; sweeping round to the side of the skull, this margin also sutures, outside the parietal lamina just mentioned, with the dorsal lamina of the squamosal bone.

The *Foramen Magnum* is bounded below by the basioccipital bone in the median one-third of its extent, and by the lower portions of the occipital condyles, on the exoccipital bones, for the other two-thirds. The lateral margins, formed by the exoccipital bones, converge towards one another dorsally, but do not meet, there being a gap in the mid-line above, this gap extending upward as a notch into the inferior margin of the supraoccipital. In the flesh it is made good by a sheet of fascial tissue.

REGIO SPHENOIDALIS

In this region there are the basisphenoid bone below and the parietal above, with the posterior portion of the composite periotic bone between them. The vestigeal alisphenoid bone is described with the facial skeleton.

The *Parietal* is a large, single bone which forms the vaulted dome of the cranial cavity, extending almost the whole width of the dorsal surface of the cranium from the supraoccipital to the frontal bones. As we have seen, its posterior border forms a transverse, serrated suture with the supraoccipital. The postero-lateral angle is overlapped by the anterior part of the expanded dorsal limb of the squamosal. Anteriorly the bone is produced on each side into a pointed process which overlies the postero-lateral corner of the frontal of its side. In the mid-line, between these larger processes, are two other, smaller, processes which underlie the posterior border of the frontal bones on either side of the sagittal suture. The lateral border of the parietal bone forms sutures with the dorsal margin of the orbitosphenoid and behind this with the dorsal edge of the alisphenoid lamina of the periotic bone.

The *Basisphenoid bone* is to a large extent hidden inferiorly by the palatine. It does not lie in the same plane as the basioccipital bone, but inclines dorsally as it extends forward. It is a quadrilateral bone with two short processes on each side. Posteriorly it sutures with the basioccipital medially and with the cochlear portion of the periotic on each side. Anteriorly it sutures with the presphenoid. The posterior of the two pairs of lateral processes have, in previous descriptions of this skull, been termed the two alae temporales, but inasmuch as it has been demonstrated that the alisphenoid is always developed from a true ala temporalis and that there is no alisphenoid developed in relation to the processes in this skull, it would appear more correct to designate this pair the *processes alares*. Each processus alaris is a short broad expansion of the bone, which sutures in the adult skull with the inferior edge of the alisphenoid lamina of the periotic. The anterior processes are narrower but of equal length, and they also form a suture with the same lamina of the periotic bone, at its antero-inferior angle. Inferiorly each processus alaris is intimately fused with the pterygoid bone and below this it forms a suture with the lateral edge of the

palatine towards the posterior end thereof, and with the vestigeal alisphenoid bone. On the inferior surface it is grooved along the mid-line for the reception of the dorsal margin of the vomer, this groove being flanked on each side by a low ridge. On either side of the groove a little way from the posterior limit of the bone there are to be seen the two external apertures of the carotid canals. Viewed from above the body of the bone is convex, with the processes alares appearing to stand out from the inferior edge of the convexity of the body. The sella is defined by lateral ridges and by a post-clinoid transverse wad. Viewed from below, the body is flat, with the alary processes standing down and out at an angle of about 45°. The pterygoid bones are plastered to the sloping lower surfaces of the processes, the slightly prominent inferior edge of the pterygoid forming with the alary process to its outer side a groove for the reception of the palatine. The inferior extremity of each alary process is somewhat thickened and is perforated along its length by the canal for the internal maxillary artery and a small nerve from the otic ganglion. The Vidian canal perforates the fused pterygoid bone and process obliquely just in front of and above the fore end of the canal for these structures. None of our skulls is young enough to allow us to speak definitely on the relation of the Vidian canal to the pterygoid bone. Watson (1916, p. 320) quotes Gaupp as stating that the pterygoid is not perforated by the nerve. In our Skull *B*, disarticulated, the canal is found above the posterior portion of the pterygoid bone, which is definable as such by reason of the fact that its ventral border is free, with a nearly obliterated suture line between it and the alary process, commencing just in front of and above the nerve where it enters the bone, and extending thence dorsally and forward across the inner side of the process till it reaches the body of the basisphenoid; this suture then becomes quite distinct and passes directly forward. It would appear from the conditions found that the canal lies between the process and the pterygoid bone throughout its length. This is practically as Watson (*l.c.* p. 331) describes the course of the nerve. This description of the basisphenoid is based on the bone in the little disarticulated 48 mm. skull, but it is actually applicable equally well to the bone in the adult skulls. Our youngest skull enables us to state that the bone ossifies from three centres, one median, and two lateral, these latter situated in the processes alares medial to the canal for the artery.

The *Periotic bone* covers in the greater part of the side of the cranium as well as forming part of the posterior wall lateral to the exoccipital and supra-occipital bones, and in the otic region is covered to a great extent by the squamosal bone. On the inferior surface of the bone, the crista parotica supplies a landmark that may well serve as a starting-point from which to describe the bone.

The crista parotica is wedge-shaped, the thick truncated end of the wedge being posterior, and the thin end of the wedge is produced forward like a flying buttress to the posterior edge of the foramen ovale by a ridge. The inner side of the truncated posterior end is notched and its point (processus styloideus)

gives attachment to the hyoid arch; in the very young skull it has been shown to be in cartilaginous continuity with Reichert's cartilage. The notch is continued forward along the inner side of the process and its buttress as the sulcus stylomastoideus. The vestibular and cochlear portions of the bone lie immediately to the inner side of the process, the labyrinthine portion of the bone is directly above it, the processus anterior, or as we would prefer to designate it, the alisphenoidal lamina, extends forward of and above it, whilst the crista parotica and a small area of the bone behind it may be regarded as constituting the mastoid portion of the bone. A parietal lamina is present above the labyrinthine portion of the bone.

The fenestra ovalis (*seu* vestibuli) lies immediately to the inner side of the anterior end of the stylomastoid sulcus on the inferior surface of the vestibular portion of the bone. The fenestra rotunda (seu cochleae) is situated further back on the vertical posterior margin of the bone in line with the posterior margin of the foramen jugulare. The cochlear portion of the bone medial to these apertures is roughly oblong; its long axis extending forwards and medially; it sutures with the lateral border of the basioccipital and the postero-lateral corner of the basisphenoid. Immediately above and behind the crista parotica there is to be seen in young skulls a prominence due to the conjoined ends of the horizontal and posterior semicircular canals, in older skulls this prominence is obscured by the greater development of the root of the crista parotica.

The stylomastoid sulcus burrows further under the crista parotica as it is followed forward until it reaches the flying buttress formed by the hinder end of the alisphenoid lamina; this is perforated for the transmission of branches of the vena capitis lateralis and of the external carotid artery, and it is this perforation which leads us to describe it as a "flying" buttress. On the anterior wall of the tunnel thus formed under the buttress the external aperture of the Fallopian canal (stylomastoid foramen) opens on to the sulcus. Looking into the Fallopian canal from here one is able to see right through into the hinder angle of the foramen rotundum owing to the fact that the hiatus Fallopii opens on to the hinder wall thereof in direct line with this lower segment of the canal. The inner aperture of the canal is within the internal auditory meatus near its anterior margin, from here it takes a short course forward, downward and slightly outward, to very nearly perforate the hinder wall of the foramen rotundum, and at this point an actual perforation results from the departure of the very short hiatus Fallopii. At the point of departure of the hiatus the canal turns abruptly backwards and with a slight downward trend reaches the external aperture situated as described. In two of our skulls there is on one side a small canal parallel with and just to the outer side of the lower segment of the Fallopian, and from the fact that it is of inconstant occurrence we conclude that it transmits blood vessels. In our Skulls *B* and *C* (48 and 50 mm.) the proximal portion of the Fallopian canal, i.e. the portion between the internal auditory meatus and the hiatus Fallopii, presents the

embryonic condition, and it is enclosed by the ossified commissura suprafacialis only. Doubtless the geniculate ganglion at this stage was lying uncovered against the posterior wall of the foramen rotundum. And moreover in the 48 mm. skull (*B*) the lower segment is not enclosed by bone below, and is only a forward continuation of the stylomastoid sulcus. There is little doubt that the geniculate ganglion in the adult skull lies in the canal at the point of departure of the hiatus and not, as Watson (*l.c.* p. 331) states, at its lower end. Watson's description is based on serial sections of a head little older than our youngest and a good deal younger than our Skull *B*. The hiatus Fallopii was correctly identified by van Bemmelen (1901).

It is of interest to note that there is a striking resemblance between the course of the canalis Fallopii of the *Platypus* and that of man and other mammals; the course is from the internal auditory meatus, above and in front of the foramina for the eighth nerve, forward and outward, and downward in *Platypus*, to the hiatus Fallopii, thence downward and backward. The two segments have, moreover, in both cases similar origins. The proximal is formed below the cartilaginous commissura suprafacialis, the geniculate ganglion lies immediately beyond the commissure. The distal segment is enclosed by extension of ossification beyond the cartilage, this extension reaching a variable distance towards the styloid process. There is no doubt that what Watson (p. 331) regarded as the outer end of the Fallopian canal is in verity the hiatus Fallopii. Actually the roof of the "sulcus facialis" is the posterior portion of an incompletely enclosed Fallopian canal. The attachment of Reichert's cartilage indicates that the apex of the "crista parotica" may be aptly termed "styloid process" to impress the homology of the part, and hence our designation "sulcus stylomastoideus" in preference to "sulcus facialis."

A comparison of the early condition of the Fallopian canal of *Platypus* with those of *Xerus* (Fawcett, 1923), *Miniopterus* (Fawcett, 1919) and *Tatusia* (Fawcett, 1921) as well as that of man (Macklin, 1921), discovers a remarkable general similarity, and, in view of the diversity of the forms mentioned, it would appear that this is the fundamental mammalian condition. There is, moreover, a general similarity to this disposition in the birds and some reptiles (Kesteven, 1925 A).

Returning again to the tunnel under the flying buttress (which, it will be remembered, lodges the vena capitis lateralis, the facial nerve and the superficial temporal branch of the external carotid artery) the external aperture of the canalis vena capitis lateralis will be found to the outer side of the stylomastoid foramen. The course of this canal is upward and slightly outward and forward through the bone just in front of the ampulla of the anterior semicircular canal, but near the top of the curve of this canal it opens into the cranial cavity, and the main branch of the vessel passes backward above the arcuate fossa in a well-marked groove. Watson describes another branch, which, he states, "splits up and seems to send branches both above and below the ganglion semilunare in the sinus cavernosus" (*l.c.* p. 336).

The mastoid portion of the bone behind and above the crista parotica sutures with the exoccipital bone. Viewed from the lateral aspect the otic capsule proper is almost entirely covered by the body and lower expansion of the squamosal bone, whilst above the capsule the dorsal expansion of the same bone covers the parietal lamina of the periotic bone. The alisphenoid lamina of the bone is very extensive. In shape it is approximately oval, the fore end of the oval being narrower than the hinder. It may be said to spring from the front of the otic capsule by a narrow neck. To the inner side of this neck is the outer angle of the foramen rotundum, to its outer side is the inner aperture of the canalis venae capitis lateralis. Above this latter point on the inner surface of the bone a groove curving forward as it rises marks approximately the fusing-point of the ossification in the membrana spheno-obturatoria and that which extends upward and forward from the processus perioticus superior. The groove in question actually lodges a forward-reaching branch of the vena capitis lateralis in the dura. It may be said then that the alisphenoid lamina of the periotic is fused to the parietal lamina above its origin from the capsule. Above the line of fusion it is in sutural contact, slightly overlapped, with the lower margin of the parietal; in front of this it forms an irregular, nearly horizontal, suture with the lower margin of the orbitosphenoid, and this suture terminates at the sphenoptic fissure. Following down the posterior margin of this fissure the lamina next forms a short suture with the anterior lateral process of the basisphenoid, it next arches over the foramen ovale to form a suture with the upper edge of the lateral margin of the processus alaris, and at the posterior end of this last process it arches over the foramen rotundum and reaches the otic capsule with which we started.

The parietal lamina is largely covered externally by the dorsal expansion of the squamosal bone. It extends dorsally and posteriorly from the superior border of the labyrinthine portion of the bone, and it is in sutural relation behind with the supraoccipital and above with the parietal.

In our two youngest skulls this last lamina is not yet developed, the whole of the dorsal expansion of the squamosal bone rests upon a thin sheet of membrane which completes the side wall of the cranium between the labyrinthine portion of the periotic bone below and the lateral edge of the parietal bone above, and also between the posterior margin of the dorsal expansion of the squamosal and the lateral margin of the supraoccipital bone on the posterior aspect of the skull. This extensive sheet is apparently an extension from the processus superior periotici and it occupies the situation of the parietal lamina of the bone in older skulls. In the young skulls in question the processus superior is ossified as a low ridge along the dorsal margin of the labyrinthine portion of the bone, the alisphenoidal lamina on the other hand is well developed, and presents the features of the adult bone on a reduced scale, the postero-dorsal margin corresponding very nearly to the vascular groove above mentioned as the line of fusion of the two laminae in the adult skull.

Before leaving the periotic bone there remains to be mentioned a small foramen close to the inner edge of the foramen rotundum at its anterior angle. In one of our skulls this appears as a notch in the margin of the foramen rotundum on the right side and as a foramen on the left, in the two youngest skulls it is represented by a notch on both sides. This foramen (foramen vasculosum innominatum) has been described as transmitting a deep temporal artery. There is a very definite vascular (?) groove extending upward and forward from it on adult skulls.

The *Squamosal bone* has been described as entering into the formation of the side wall of the cranium by its dorsal lamina; this, however, is an error which the material we have enables us to correct. The disarticulated bone in Skull *B* presents a zygomatic process, a body, a dorsal and a ventral lamina, the latter divided into anterior and posterior portions (fig. 2). The zygomatic process is grooved along its length inferiorly for the reception of the zygomatic process of the maxilla. The body, approximately square in outline, is no thicker

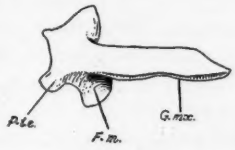

Fig. 2.

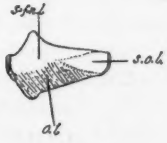

Fig. 3.

For explanation see text.

than the rest of the bone, though appearing more solid when in position owing to the fact that it is broadly grooved antero-posteriorly to form the outer wall of the post-temporal canal between itself and the outer wall of the otic capsule. The form of dorsal and ventral expansions is plainly shown in the figure and calls for no description.

In Skull *C* the bone is of almost precisely the same size and shape as that in Skull *B*. The inferior or ventral lamina lies directly against the outer aspect of the labyrinthine portion of the periotic bone, the little bay between the anterior and posterior portions of the lamina clasping a prominence on that bone which is due to the underlying posterior vertical semicircular canal. The lower half of the inner wall of the post-temporal canal is formed by the ossified processus superior periotici, the upper half by a sheet of membrane directly implanted on its dorsal free margin. This sheet of membrane finds attachment behind to the lateral margin of the supraoccipital bone, in front it is continued forward along the dorsal free margin of the alisphenoid lamina of the periotic and gains attachment to the posterior angle of the orbitosphenoid bone. Superiorly the membrane is attached to the lateral margin of the parietal just within its actual edge. In this dried partially disarticulated skull there is a definite gap between the dorsal lamina of the squamosal bone and the membranous sheet. Quite certainly then the dorsal lamina was not developing in this membrane but external to it. On placing the parietal bone

in place it is found to be overlapped at its postero-inferior corner by the dorsal lamina of the squamosal bone.

In Skull *D*, though very little larger, the squamosal bone has assumed the full adult form and relations. There is very little actual enlargement of the bone in any of its parts, but it is now in sutural relation to the supraoccipital bone. This latter has expanded, doubtless by ossification of the sheet of membrane, so that there is now no interval between it and the periotic bone below and the dorsal arm of the squamosal in front. An examination of the inner wall of the cranium fails to discover anything that may be regarded as a suture between the old level of the ossified processus superior periotici and the margins of the parietal and supraoccipital bones. An examination of the cross-section of the fractured suture between the dorsal arm of the squamosal and the parietal and of the dorsal arm itself and the bones in front and behind it, parietal and supraoccipital, reveals that there are very clearly two fused layers of bone along the section of the dorsal arm and only one along the sections of the other bones.

There is no longer any division of the ventral arm of the squamosal into anterior and posterior portions, the little bay has been filled in and the prominence of the inferior end of the semicircular canal masked by a general thickening of the bones of the skull in this region.

In the young adult skull *E* the only differences are of size.

It is concluded that the squamosal bone does not enter into the formation of the cranial wall, but is excluded therefrom by the parietal lamina of the periotic bone which underlies it and with which very early in adult life it becomes intimately fused.

In the *presphenoid* and *ethmoid regions* the axis of the skull is ossified by extension from the orbitosphenoid bones. In Skull *B* the orbitosphenoid bones have the form shown in fig. 3. The long axis of this little bone is directed antero-posteriorly, and the broader end is the front, the ventral margin having the larger expansion. Actually the two lateral expansions of the bone anteriorly lie in planes nearly at right angles to one another. In Skull *C* the orbitosphenoid has almost precisely the same shape and size as that of Skull *B*. It lies in place with the dorsal anterior expansion almost entirely overlapped by the hinder end of the frontal bone, and behind this bone the dorsal margin is in contact with the lateral edge of the parietal. The thickened posterior end gives attachment to the anterior edge of that sheet of membrane above described as being later ossified from the two processes of the periotic bone. The lower margin of the bone behind the anterior lateral or ventral expansion is in contact with the anterior part of the superior margin of the alisphenoid lamina of the periotic. The lateral expansion (ala orbitalis) of the orbitosphenoid reaches down in the vertical plane to the level of the skull base, and its ventral edge or corner is attached to a sheet of cartilage which extends across the cranial floor to become attached in similar manner to the opposite orbitosphenoid. This sheet of cartilage is of particular interest. In front of the

orbitosphenoid bones it continues forward for a short distance and then is split into three narrow bands. Of these the median rises in the sagittal plane in the mid-line, and is the cartilaginous septum nasi; it is interrupted almost at once by the internarial hiatus which persists in the bony septum of the adult. The lateral bands pass forward from the outer corners of the main sheet, attached to the upper border of the orbital plate of the palatine bone and in front of this to the inner aspect of the maxilla, below the level of the naso-lachrymal and infraorbital canals and above the ophthalmic nerve. In front of the foramen ophthalmicus posterior this lateral band of cartilage gains attachment to the nasal bone above and to the inner side of the canalis ophthalmicus, and to the maxilla below that canal, continuing forward with these attachments to the foramen ophthalmicus anterior at the forward limit of the palatine plate of the maxilla. Throughout its length it spreads out over the inner face of the maxilla below the actual line of attachment, so that it supplies a lining to the lateral wall of the nasal cavity from the roof thereof almost to the floor.

Behind the ventral processes of orbitosphenoid bones the sheet of cartilage is attached to the upper margins of the pterygoid bones and by them is carried back to gain attachment to the fore end of the basisphenoid bone across the mid-line. It is noteworthy that this sheet of cartilage, which forms the floor of the cranial cavity and roof of the naso-pharyngeal cavity in the presphenoidal and ethmoidal regions, is absolutely devoid of any trace of centres of ossification, at a time when every bone in the skull except the ethmoid and the presphenoid is assuming the form of the bones of the adult skull.

In our next stage, Skull *D*, which, it will be remembered, is very little larger than *C*, the whole of this sheet of cartilage has been ossified (fig. 4).

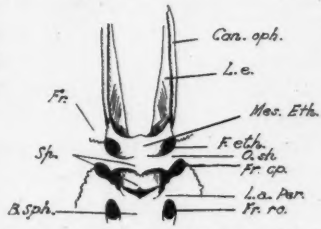

Fig. 4. Semi-schematic drawing of presphenoid and ethmoid of *Platypus*. For explanation see text.

Seen from the lateral aspect, the orbitosphenoid now extends further back below the parietal bone and above the alisphenoid lamina of the periotic. The amount of this extension is not as great as it appears to be. In Skull *C* the posterior limit of the bone is vertically above the hinder margin of the foramen ovale, in Skull *D* the posterior limit is a little further back, but the alisphenoidal lamina has extended forward and below it. In front of the sphenoptic fissure the orbitosphenoid bone is seen extending down to suture with the fore end of the pterygoid, the upper margin of the orbital lamina of the palatine and the postero-inferior corner of the orbital plate of the frontal bone. Above these sutures the bone is grooved to form the sulcus pro nervi ophthalmici. This sulcus may be described as being terminated by the foramen ophthalmicum. Looking into this foramen it will be found that there is an hiatus in the side wall of the skull immediately to its inner side; this is the

fenestra ethmoidale. The suture between the orbitosphenoid bone and the orbital plate of the frontal runs vertically upward from the ethmoid fenestra and is interrupted just below the supraorbital margin by a foramen which transmits an ethmoid artery. Within the foramen the artery apparently breaks up into a posterior diploic branch and an anterior larger branch, which splits again into branches to the canal for the nervus ophthalmicus and the posterior region of the nasal chamber in the neighbourhood of the turbinate bones; at least it may be stated confidently that the foramen in question has communications suggestive of this division of the transmitted vessel, and it may be designated foramen ethmoidale superius.

Turning now to the interior of the cranium it will be seen that the two ventral processes of the orbitosphenoid bones are joined across the mid-line by a narrow bar of bone. This bar of bone is incorporated into the plate of bone which has replaced the sheet of cartilage that in Skull *C* here formed the floor of the skull and roof of the naso-pharyngeal passage. No trace of suture is discernible anywhere in this fusion.

The conjoined ends of the ventral processes of the orbitosphenoid bones are, in this skull, flush with the plane of the plate of bone forming the skull floor, but at their point of attachment on either side, coming down as they do from above, they clearly mark a "step up" that, in the next stage, is developed right across the floor. The portion of the plate behind and that beneath the "step" may be regarded as presphenoidal topographically, whilst that in front of it is ethmoidal, in the same sense. The extent of the horizontal portion of this plate anteriorly is greater than was that of the sheet of cartilage which it has replaced, and it has been extended upward as well as forward so that the vertical bar which is the posterior end of the septum nasi is shorter than was the cartilaginous bar. This piece of the bone is nearly in contact with a low ridge developed on the under side of the fore end of the frontal bones along the sagittal suture. The lateral processes, too, are shorter, as viewed from behind, than were their cartilaginous precursors; they are in contact with the inner face of the maxilla, separating the fenestra olfactorius from the canal of the ophthalmic nerve. Laterally the plate is attached to the inner face of the maxilla, roofing the infraorbital canal, and to the nasal bone, forming the inner wall of the ophthalmic canal.

In Skull *E* the adult conditions are nearly approached.

There is a small hiatus between the hinder end of the presphenoidal plate and the fore end of the basisphenoid bone. On either side of this hiatus the dorsal edges of the pterygoid bones appear. In front of the hiatus the ophthalmic sulci appear as though encroaching on the cranial floor. Where these sulci pass under the ventral plates of the orbitosphenoid bones the cranial floor is markedly stepped up, and from here forward there is a steady even rise to the point of contact with the frontal bones. Owing to the presence of the fenestrae ethmoidalia and the fact that the sulci for the ophthalmic nerves lie beneath the cranial floor it appears as though there were four apertures in the fore end

of the cranial cavity; those on either side of the mid-line are the fenestrae olfactorii, the outer pair are the canals for the ophthalmic nerves seen through the ethmoidal fenestrae. The constriction of the cranial cavity initiated at the posterior margin of the ventral processes of the orbitosphenoid bones becomes accentuated at their anterior margins; here a very definite ridge takes origin on each side and swings upward and slightly forward across the processes to the roof of the cavity, and these constitute a very definite boundary line between the cranial cavity proper and a true *sphenoidal cavity* in front (Kesteven, 1925 B, p. 280).

That process of the frontal bones, which in the last stage was nearly in contact with the fore end of the ethmoidal plate, has in this stage developed further down and is now in contact. We have carefully opened the roof along one side of the sagittal suture and cannot persuade ourselves that this little *ethmoidal process of the frontal bones* is other than that name implies.

The fenestra ethmoidale is still present, as already noted above.

Forward of the olfactory fenestrae the inner walls of the canal for the ophthalmic nerve, and of the infraorbital canal below it and a little further from the mid-line, together constitute the outer wall of the nasal cavity. There are here three sets of turbinate bones. The upper set is much the smaller and is placed high up on the wall just in front of the olfactory fenestra. The middle set is placed at a lower level just in front of the fore end of the first set and extends forward to about the junction of the posterior and middle thirds of the length of the snout, or nearly half-way to the position of the external nares. The lower set is small with one element extending forward to the anterior olfactory foramen.

In the old adult skull *F* there is a general resemblance to Skull *E*. One notes the closure of the fenestra ethmoidale and a general increase in thickness of the bones, as well as the complete closure of all the sutures except that between the fore end of the ethmoidal plate and the ethmoidal process of the frontal bones.

Reviewing now the features observed it is apparent that the presphenoid and ethmoidal regions have been ossified by extension from the orbitosphenoid bones and that these bones cannot be defined genetically. It is, however, quite open to us to define not only the orbitosphenoid bones but also the presphenoid and ethmoid on a topographical basis.

The extent of the orbitosphenoid bones has been correctly determined by previous authors. The presphenoid may be regarded as constituting the cranial floor from the fore end of the basisphenoid to the posterior boundary of the sphenoidal cavity.

The ethmoid is a much more extensive bone. It forms the floor of the sphenoidal cavity and supplies the side walls of the nasal cavity as far forward as the anterior opening of the canal of the ophthalmic nerve.

The persistence of the suture between the fore end of the ethmoidal plate and the ethmoidal process of the frontal bones, taken in conjunction with

the situation of the anterior continuations of the ethmoidal cartilage, together clearly indicate that van Bemmelen erred in his interpretation of this region of the *Platypus* skull. His sections (1901, p. 744) indicate an ethmoid continuous across the roof of the nasal cavity just in front of the hiatus in the septum nasi. Our material enables us to state quite emphatically that this is not so, and we have endeavoured to convey the situation and relations of the ethmoid in the drawings of the nasal region of the skull in a later section of this paper (see also Watson's fig. 19, p. 336).

The *Frontal bone* develops very early, even in our youngest skull it presents in miniature most of the features of the adult bone. The dorsal and orbital plates are well developed, the connecting isthmus being largely covered by the antero-lateral corner of the parietal just as in the adult skull.

In the adult the dorsal lamina sutures in front with the nasal bone and behind and laterally with the parietal bone. In the 48, 50 and 65 mm. skulls the antero-lateral corner of the parietal bone reaches the postero-lateral corner of the nasal of each side, covering the outer portion of the dorsal lamina of the frontal and the isthmus connecting this latter to the orbital plate. In the 80 mm. skull, and, as far as one can judge, in the adult skulls as well, though a portion of the dorsal lamina is similarly covered, the isthmus is freely exposed on the surface of the skull. The orbital plate is situated on the inner wall of the orbit in front of, and below, the hinder margin of the isthmus. Its superior margin sutures with the lateral margin of the nasal, and its anterior border forms a short suture with the orbital process of the maxilla. Inferiorly this short suture is interrupted by the lachrymal foramen. Immediately below this foramen the orbital plate forms an even shorter suture with the dorsal edge of the lachrymal bone, and behind this the inferior margin sutures with the dorsal margin of the orbital plate of the palatine bone. The posterior margin of the orbital plate sutures with the anterior margin of the ala orbitalis of the orbitosphenoid bone. This suture is interrupted by the foramen sphenoidale superius immediately below the orbital margin and a little lower it is more drastically interrupted by the foramen ophthalmicum (foramen ethmoidale of van Bemmelen), and below this latter the inferior margin sutures with the outer edge of the presphenoid bone. The portion of the plate interposed between the presphenoid above and to the inner side and the orbital plate of the palatine below appears as a little backward-projecting tongue; the tip of this tongue is in sutural contact with the anterior tip of the pterygoid bone, and just where these meet, between them and the presphenoid, to the inner side, there is fairly constantly a vascular foramen (foramen sphenoidale inferius). It should be noted that the orbital plate of the frontal bone does not enter into the formation of the cranial wall, but forms the outer wall of the ophthalmic canal and a portion of the inner wall of the orbit, separating the former from the latter.

THE FACIAL REGION

The *Nasals* are elongated flat bones which roof in the major portion of the nasal cavity and form part of the side wall thereof as well. They overlap the frontals behind and suture with the maxillae and premaxillae laterally, meeting one another in a long median suture. Anteriorly they become narrower and diverge. In the disarticulated skull it is seen that the bones are deeply grooved to form the greater part of the length of the ophthalmic canal. There are two exits from this canal, the *foramen ophthalmicum superius* interrupts the naso-maxillary suture a little way in front of the orbit, the *foramen ophthalmicum anterius* appears as an elongated sulcus at the fore end of the nasal bone lateral to the prevomer or dumb-bell bone. Though it would appear so to do the nasal bone does not actually supply a side wall to the nasal cavity except near the fore end, because the delicate ethmoid is plastered to it almost as far forward as the posterior end of the prevomer. In front of the prevomer the nasal bones extend forward to fit against the posterior border of the inturned ends of the premaxillae, and for the greater part of this length they appear on the inner side of the premaxillae on the inferior aspect of the skull. Between the diverging ends of the nasal bones the dorsal surface of the anterior point of the palatine plates of the maxilla is visible covered by cartilage and with the prevomer just a little further forward embedded in the cartilage.

The *Lachrymal bone* is apparently present as an independent entity in our youngest specimens. Here we find a trihedral piece of bone placed in the angle of the maxilla formed by the junction of the malar process and the body. The little bone lies just within the antorbital ridge below and behind the orbital process of the maxilla and rides on the dorsal edge of the root of the malar process, forming the roof of the posterior infraorbital foramen. The bone sutures with the root of the malar process on the outer side and with the anterior edge of the orbital plate of the frontal on the inner side. Where these two sutures meet the lachrymal foramen is to be found, and from this the suture between the orbital plate of the frontal and the orbital process of the maxilla passes directly upward.

The suture across the roof of the infraorbital canal is not so evident. Though we feel confident on the point we do not care to speak dogmatically thereon, and therefore make the announcement of this discovery with a little reservation. The suture between the lachrymal and the orbital plate of the frontal is the most persistent and has, in the past, been regarded as being between the orbital process of the maxilla and the plate of the frontal. The condition, as we describe it, is similar to that of *Aelurus* and *Ursus* (Gregory, 1920, pp. 148 and 151, figs. 81 and 82).

With rather more hesitation we express the opinion that future investigation will demonstrate an original independence for the little piece of bone which in *Echidna* is found between the lachrymal foramen and the posterior

infraorbital foramen, attached to the root of the malar process but sutured to the orbital plate of the frontal.

The *Maxilla* may, for descriptive purposes, be said to be composed of a body and palatine and malar processes. The body is situated in the side of the face in front of the orbit, it sutures above with the nasal and premaxilla, both to its inner side, and below with the premaxilla. The body is thinner from above downward in front than it is behind, where it is tunnelled by the infraorbital canal; actually this canal tunnels nearly the full length of the bone, but it is very much reduced forward of the infraorbital foramen, which is a large opening situated on the side of the bone a little in front of and below the superior ophthalmic foramen. The anterior infraorbital foramen will be found at the extreme anterior tip of the body of the maxilla on the inferior aspect of the skull. The postero-dorsal corner of the body forms part of the anterior boundary of the orbit and has been referred to above as the orbital process of the bone. The palatine process of the maxilla is a long narrow lamina attached to the infero-medial border of the body, but leaving it in front to permit of the insertion of the palatine process of the premaxilla. At about the centre of the length of the palatine process the line of attachment to the body is interrupted by the inferior infraorbital foramen. The anterior extremity of each palatine process is deeply notched, and it is the common projection of the two processes between these notches which appears between the diverging anterior ends of the nasal bones when the skull is viewed from above. The posterior margins of the palatine processes suture with the anterior margins of the palatine bones.

The malar process springs from the postero-lateral corner of the body, and immediately spreads out below into the wide, spoon-like dental fossa. No trace of this fossa is visible in our youngest skull and it is little more than indicated in the 48 mm. skull. Behind the fossa the malar process continues as a laterally compressed splint bevelled on the inner side superiorly for suture with the forward-extending malar process of the squamosal bone.

The *Jugal* is a little triangular splint of bone which is perched on the dorsal edge of the zygoma, just above the anterior end of the squamosal component thereof. This little bone marks the boundary between the orbital and temporal fossae. In old adult skulls it becomes completely merged with the other components of the zygoma, and its dorsal edge bears backward and inward, very clearly indicating the outer one-third of the posterior boundary of the orbit. Beyond this there is nothing in the skull to indicate the boundary between the two fossae.

The *Premaxillae* are elongated bones which, for the greater part of their length, fit in between the nasal bone and maxilla on the upper aspect of the skull. Inferiorly the same relations are maintained forward of where the bone fits between the palatine process and the body of the maxilla.

The body of the *Palatine bone* is oblong in outline, it sutures in front with the hinder margin of the palatine plate of the maxilla, laterally it sutures with

the dental plate of the same bone and behind this its lateral margin is free for about one-third of the total length of the bone. Behind the free margin the bone sutures with the inferior edge of the processus alaris above it and with the vestigeal alisphenoid below it. The posterior margin of the bone is free, lying below the posterior choanae. The orbital lamina of the palatine bone is a thin plate of bone, broader in front than behind, which rises in the vertical plane from the dorsal surface of the bone near its lateral edge. Anteriorly this lamina is in sutural contact with that part of the posterior end of the body of the maxilla which forms the inner wall of the infraorbital canal. Above this there is a point of suture with the lachrymal, and then the dorsal margin of the lamina sutures with the ala orbitalis of the frontal and behind this with the inferior edge of the anterior end of the pterygoid bone. In our 48 and 50 mm. skulls there is on the dorsal surfaces of the palatine bones close to their medial borders a pair of para-vomerine laminae, which together form a trough into which the vomer is fitted when, at a later stage of development, it is formed from the cartilaginous septum which at this stage occupies its place. It is noted that the palatine bone extends almost to the posterior end of the processus alaris and well beyond the posterior limit of the pterygoid bone.

The *Alisphenoid bone* is represented by the tympanic wing only in the Prototheria; in the past this little bone has been designated "Echidna-pterygoid," following the lead of Gaupp (1905 and 1910), but in conformity with the conclusions of the senior author (Kesteven, 1918) that term is discarded in this paper.

The bone in the *Platypus* is an elongated spathulate splint, broader and thinner in front, quite loosely sutured to the inferior aspect of the suture between the processus alaris and the palatine. The anterior end stands out freely lateral to the palatine bone below the foramen rotundum. The posterior end of the bone stands beyond the palatine and is produced into a small hook which lies in the same plane as the rest of the bone and therefore is inclined downward and away from the mid-line of the skull. This hook is attached along its posterior edge to the anterior extremity of the curved tympanic bone by a ribbon of connective tissue.

Although this bone presents few of the relations detailed for the so-called Echidna-pterygoid in *Echidna* by the senior author in the communication above referred to, and on which the conclusions therein arrived at were based, still its position is such as to leave no room for doubt as to its complete homology with that bone and also justifies our use of the designation "tympanic wing of the alisphenoid bone."

The *Pterygoid bone* has been described above in the course of the description of the basisphenoid.

The *Prevomer* has been so frequently and so fully described that it is not necessary to discuss it here, and the same holds true for the vomer.

THE NERVE AND VASCULAR CANALS AND FORAMINA, AND OTHER FENESTRATIONS

The *Foramen Magnum* is bounded below by the basioccipital only in the young skulls, but in adult skulls the foramen is relatively much enlarged by absorption of the lamina of the exoccipital bone on each side above the condyles, which latter come thus to bound the adult foramen magnum inferiorly. The lateral boundaries are supplied by the exoccipital bones, and these, converging, nearly meet above. There is a gap above the foramen, between the exoccipital bones and the supraoccipital above them; this is filled, in the flesh, by a strange fascial membrane.

The *Foramen Jugulare* is bounded medially by the basioccipital, and in front by the periotic and behind by the exoccipital, these two latter bones meet at the outer angle of the foramen. It would appear that all the cranial nerves behind the eighth leave the cranium through this foramen.

The Fallopian canal and hiatus, the internal acoustic and the external acoustic apertures have already been sufficiently described.

The *Foramen Ovale* lies between the vestibular portion of the periotic and the hinder angle of the basisphenoid to the inner side, and the lower margin of the alisphenoid lamina of the periotic to the outer side; it transmits the third branch only of the fifth nerve.

The *Foramen Rotundum* is bounded to the inner side by the body of the basisphenoid, in front by the antero-lateral process and behind by the processus alaris of the same bone. Its outer boundary is the lower margin of the alisphenoid lamina of the periotic bone. The second branch of the fifth nerve finds its exit from the cavity through this foramen.

The *Sphenoptic Fissure* (Kesteven, 1918, p. 466) is bounded below and behind by the anterior corner and antero-lateral process of the basisphenoid; in front of these its inferior boundary is the edge of the body of the presphenoid and the dorsal margin of the pterygoid meeting in sutural contact. The antero-superior margin is the descending process of the orbitosphenoid. The postero-superior margin is the antero-inferior corner of the alisphenoid lamina of periotic bone. Between these two latter there is, in all but fully adult skulls, a deficiency (fenestra sphenoidale, fig. 5, *F.sp.*) in the side wall of the skull, made good by the remnant of the membrana spheno-obturatoria.

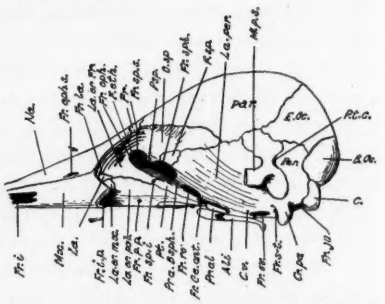

Fig. 5. The letters *Fr.oph.* point to the anterior end of the sulcus ophthalmicus. The nerve leaves the brain case in the lower angle of the foramen sphenopticum.

The sphenoptic fissure transmits the optic, the third, fourth and sixth nerves and the first branch of the fifth nerve.

It may be noted that Watson (p. 334) states that the "ophthalmic and maxillary branches of the trigeminus leave by the anterior part of the sphenoparietal fissure." The statement is, of course, based upon the conditions in a young individual before the junction of the anterior corner of the alisphenoid lamina of the periotic and the antero-lateral process of the basisphenoid divided the sphenoparietal fissure into foramen rotundum and sphenoptic fissure. (This division is referred to at greater length further on, in a note on the fate of the Taenia clino-orbitalis.) A little further on Watson states of the first branch of the fifth nerve that it passes through the orbito-nasal fissure and immediately enters a canal in the paries nasi, and his fig. 19 shows it passing forward surrounded by cartilage. Our older, but still young, skulls would seem to demonstrate that the cartilage intervening between the nerve and the nasal bone is absorbed; we have been unable to find any cartilaginous lining to the ophthalmic sulcus along the nasal bone.

The *Olfactory Foramina* lie close together at the front of the sphenoidal cavity, separated by the little spur of the ethmoid which sutures with the two frontal bones. The lateral boundary of each is the short lateral process of the ethmoid which joins the nasal lamina thereof to the body of the bone.

The positions of the foramen for the internal carotid artery, and for the superficial temporal and internal maxillary branches of the external carotid, have already been described, as also has the course of the vena capitis lateralis through the periotic bone.

The side wall of the naso-pharynx is perforated by two apparently constant vascular foramina. One of these, the foramen sphenoidale inferius, has been described in the course of the description of the frontal bone. The other, situated lower down and a little further forward, passes straight through the palatine bone to the palatine foramen, which latter interrupts the maxillo-palatine suture near the anterior end thereof. This posterior aperture of the palatine foramen may be designated *foramen palatinum posterius*. It should be mentioned that though the palatine foramen appears to interrupt the maxillo-palatine suture it is really entirely surrounded by the palatine bone.

The *Fenestra Ethmoidale* is a deficiency in the wall of the sphenoidal cavity between the orbital plate of the orbitosphenoid and the body of the ethmoid, and in adult skulls it is made good by ossification of the membrane present in the younger skulls. This ossification leaves no trace of suture and, judging from the gradual reduction in size presented in our series, would seem to take place from all round the fenestra.

The *Infraorbital canal* lies entirely in the maxilla. The entrance to the canal, *foramen infraorbitale posterius*, lies immediately medial to the root of the malar process of the bone. Of the three exits two have already been described, the third, *foramen infraorbitale inferius*, will be found as a large foramen continued forward as a fairly deep groove along the under surface of the palatine plate of the maxilla close to its junction with the body of the bone about the middle of its length.

The *Foramen Ophthalmicum*, which van Bemmelen designated foramen ethmoidale[1], is bounded laterally by the orbital plate of the frontal bone, below, medially and above it is bounded by the body and short lateral process of the ethmoid. From here the ophthalmic canal continues forward, first against the facial lamina of the maxilla and then in the groove in the nasal bone already described. Through its length the inner wall, beyond the actual opening, is formed by the delicate nasal lamina of the ethmoid. The exits from this canal have been described in connection with the description of the nasal bone.

THE FATE OF THE TAENIA CLINO-ORBITALIS

Wilson (1906) has already described in detail the fate of this interesting little bar of cartilage in both *Echidna* and in the *Platypus*, but, although he has pointed out that van Bemmelen is correct in his designations foramen rotundum and foramen spheno-orbitale opticum, he has not quite clearly indicated the relation of these to the fissurae parietale and pseudo-optica of the primordial cranium.

The fissura pseudo-optica persists entire in the adult skull of *Echidna*, or at least it so persists in the young adult, as evidenced by one in the possession of the senior author.

In this skull the sella is bounded laterally by two sharp ridges which become higher as they pass forward; diverging along the sides of the sella, the angle of divergence increases at the forward limit thereof. These ridges, which van Bemmelen termed middle clinoid processes and which Wilson has shown to be the ossified taeniae clino-orbitales, now slope downward (ventrally) and pass along the side of the presphenoid bone, to terminate at the inner corner of the ala orbitalis of the orbitosphenoid bone. Just in front of the anterior limit of the sella each ridge is lifted free of the presphenoid bone for a short distance, and the resulting foramen is the fissura pseudo-optica. To the outer side of and below the anterior end of the ossified taenia, on each side, there is formed a more or less complete pseudo-optic canal whose external aperture, if the canal be complete, is to be found within the antero-medial angle of the sphenoptic fissure. The large spheno-parietal fissure lateral to the pseudo-optic fissure is divided into foramen rotundum behind and sphenoptic fissure in front.

In none of our *Ornithorhynchus* skulls is there any remnant of the taeniae clino-orbitales, but Wilson has described their situation in the adult skull. Here also it will be found, on reference to his description, that the fissura pseudo-optica persists, completed by fibrous tissue, in the adult skull, and that it is situated in a precisely similar position to that of *Echidna*.

The fissura pseudo-optica, then, in the adult skull, is situated immediately above the suture between the body of the basisphenoid and the body of the

[1] Van Bemmelen's designation is discarded because it describes neither the situation nor the content of the foramen.

presphenoid on the floor of the cranial cavity, and is entirely distinct from the fissures and foramina in the side wall of the skull.

The foramen sphenopticum (spheno-orbitale opticum of van Bemmelen) is the anterior portion of the spheno-parietal fissure and although it does not include the pseudo-optic it transmits the two nerves which pass through that fissure as well as the fourth, sixth and first branch of the fifth nerves.

The foramen rotundum is the posterior portion of the spheno-parietal fissure, separated from the remainder by the union of the alisphenoid lamina of the periotic with the antero-lateral process of the basisphenoid bone.

THE CONSTITUTION OF THE NASAL CAVITY AND BONY NASO-PHARYNX

A complete bony palate extends from the anterior extremity of the maxilla right back to below the middle of the length of the basisphenoid. Of this, the nasal floor is that portion extending back to the level of the posterior boundary of the dental fossa, behind where the palate forms the floor of the post-nasal passage.

The floor of the nasal passage is formed by the palatine plates of the maxillae and by the anterior one-third of the palatine plates of the palatine bones. The roof is formed entirely by the nasal bones. The lateral walls are formed by the lateral, nasal, laminae of the ethmoid behind and by the nasal bones in front. The septum is constituted by the short mesethmoid behind the hiatus and by the vomer in front thereof.

The floor of the naso-pharynx is formed entirely by the palatine laminae of the palatine bone, the roof by the ethmoid, presphenoid and the body of the basisphenoid. The lateral walls are formed by the orbital laminae of the palatines, the pterygoid bones and the inner face of the processus alaris of the basisphenoid bone.

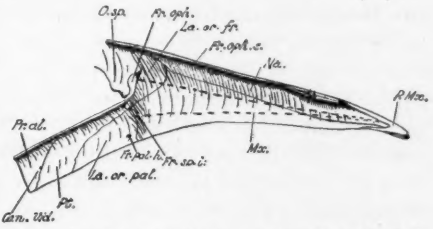

Fig. 6. The side wall of the nasal cavity and of the naso-pharynx with the cartilaginous ethmoid removed.

In fig. 6 we have illustrated, somewhat diagrammatically, the inner wall of the nasal region and of the naso-pharynx of our specimen ***B***. In this specimen there is no ossification of the cartilage of the presphenoid and ethmoid regions.

The concave face of the nasal bone is exposed along the length of the nasal cavity; this is, of course, the sulcus ophthalmicus of this stage, and the foramen ophthalmicum superius is seen perforating the bone towards the hinder end well up under the roof. The premaxilla is shown embracing the fore end of the nasal bone, and behind this the inner lamina of the facial portion of the maxilla is seen to constitute the greater part of the side wall of the nasal region at this stage of development. The position of the infraorbital canal outside this

lamina is indicated by the heavy dotted lines. Behind the maxilla the orbital laminae of the frontal and palatine are seen. The former is really situated on the outer side of the ophthalmic nerve, whilst the latter forms the side wall of the anterior part of the naso-pharynx; just at this point the bones are inclined towards the observer, so that the lateral wall of the naso-pharynx is nearer the mid-line than is the lateral wall in the nasal region. The pterygoid bone is next seen, above the orbital lamina of the palatine; the posterior portion of this bone is plastered to the inner face of the processus alaris, the postero-superior corner of which is seen at the hinder end of the naso-pharynx. The suture line between the pterygoid and the processus alaris is interrupted by the posterior foramen of the Vidian canal. Though not able to speak definitely on the point, we believe that we have correctly represented the suture. The foramen sphenoidale inferius is seen at the top of the suture between the ala orbitalis of the frontal and the anterior end of the pterygoid. The foramen palatinum posterius is seen perforating the orbital plate of the palatine bone low down near its anterior border.

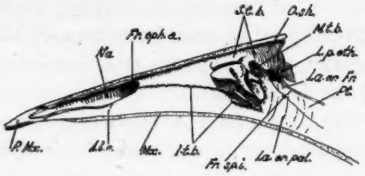

Fig. 7. The side wall of the adult nasal cavity showing the lateral ethmoid and turbinate bones.

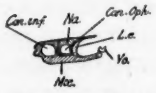

Fig. 8. A diagrammatic cross-section of the snout behind the infraorbital foramen.

In fig. 7 we have illustrated, again somewhat diagrammatically, the side wall of the nasal passage of the old adult specimen *J*. The lateral ethmoid now closes the ophthalmic canal for a little over half the length of the nasal bone, and covers the surface of the maxilla to a great extent. We have not attempted to indicate the posterior limit of the lateral ethmoid, but suggest that it is somewhere about the posterior limit of the maxilla. The anterior limit is indicated with a little more confidence by the dotted line below the ophthalmic sulcus. The lateral wall of the sphenoidal cavity is shown above the cut edge of the lateral process of the body of the ethmoid.

The superior turbinate bones are three in number. Two are but small ridges almost in line with the cut edge just mentioned, the third, a little larger, is situated further forward, above the middle turbinate. This last is more complicated, but we have endeavoured to indicate its form in the drawing. The inferior turbinate series consists of three little ridges below the middle turbinate and one, much longer, which extends right forward to the margin of the foramen ophthalmicum anterius.

In fig. 8 we have indicated, quite diagrammatically, the constitution of the snout just behind the infraorbital foramen.

THE SIGNIFICANCE OF THE ALISPHENOID LAMINA OF THE PERIOTIC

Reviewing the facts of the origin of the alisphenoid bone throughout the Craniata, in a recent contribution (Kesteven, 1926) I stated: "In every case in which its development has been studied it has been shown to develop from cartilage which is either continuous with that of the rest of the chondrocranium from its first appearance, or very early becomes continuous therewith. In the lower Craniates it has been shown that this bone is ossified indifferently from centres of ossification either in front of or behind it. In the higher forms it is seen to ossify from its own specific centre" (p. 129). I regarded the bones as always truly homologous, however arising, and proposed to recognise the difference in origin by the designations "predeterminate" as applied to those arising in continuity with other bones, and "determinate" as applied to those arising from their own specific centres of ossification (p. 121).

Throughout the communication quoted the term "lower Craniata" was used as applying to the Fishes and Amphibians, but the present study has convinced me that in the Prototheria both predeterminate and determinate alisphenoids are present. It might appear, then, that the two structures cannot be homologous, but I am of the opinion that such an appearance is deceptive, and that they are dissociated portions of the same bone.

In the first place it must be remembered that the Prototheria are truly aberrant beasts and present a very special case; it were therefore foolish to attempt to analyse the mass of evidence presented by the rest of the Craniates, using the condition in the Prototherians as the indicator, whereas the converse is only reasonable.

Briefly the position may be stated thus. Throughout the whole of the Craniata the alisphenoid, when present at all, is a bone which develops, for the most part, in membrane. In some cases the ossification of this bone is by extension from the ossifying cartilage to which the membrane is attached either in front or behind ("predeterminate alisphenoid"), in other cases the process of ossification commences in a little pellicle of cartilage which may or may not be attached to the cranial axis below ("determinate alisphenoid").

In the Marsupialia and some Insectivora the ossification in membrane is continued back below the periotic bones to form a "tympanic wing." This wing may well have been handed down from the promammalian stock, for it is well developed in certain Cynodonts.

The alisphenoid lamina of the periotic bone of the Prototheria satisfies all the conditions of the predeterminate alisphenoid, whilst the "Echidna-pterygoid" presents all the relations of the tympanic wing.

One can do little more than speculate as to the cause of the separation of the two parts of the bone, the most tempting suggestion is that the early extensive development of the palatine posteriorly resulted in the observed discontinuity. In the Insectivores and whales with an abnormal backward extension of the bony palate the formation of the posterior segment is actually

formed from the alisphenoid-pterygoid partnership, and the palatine does not extend behind the normal limit. It is an undoubted fact that the early extensive backward development of the palatine in *Echidna* and the *Platypus* has prevented the free development of the pterygoid, and one might therefore argue that, as pterygoid and alisphenoid bone are closely related at their inception, anything which interferes with the growth of one may do likewise with the other. It is obvious that, were the alisphenoid normally developed in the prototherian skull, it would not present the usual mammalian relation to the pterygoid. It may be, then, that we have here the explanation we seek.

There is another aspect of the matter that calls for comment. Is the predeterminate alisphenoid of the Prototheria to be regarded as an archaic feature or as the direct converse? These beasts present so many undoubted archaic features that one is tempted to regard the condition of the alisphenoid as another of them, but further consideration of the subject would seem to lead one to the converse conclusion.

The predeterminate alisphenoid bone of the Fishes and of the Amphibians is developed from the remnant of the complete cartilaginous cranium of the early Craniate. It should be remembered that this form of alisphenoid is found in the more archaic Fishes Crossopterygii and Holostei, which undoubtedly stand closer to the main trunk of the tree of evolution which, in its later branches, bore the Amphibians and higher Vertebrates than do the greater number of the recent Fishes. Whichever of those later branches we study we find that the primordial cranium is continuously reduced and its place taken by bones developed more and more in membrane. With the acquisition of the power of forming bone in membrane, the cartilaginous basis is more and more dispensed with. In the Fishes the alisphenoid bone develops in the cartilage of a tolerably complete primordial cranium, in the Reptiles it develops from one of the bars of an extensively fenestrated primordial cranium, whilst in the Mammals this bar has been fragmented and is represented by a mere pellicle of cartilage, the ala temporalis (Kesteven, 1926). It may well be that the Prototheria, archaic though they be in many respects, present a further stage of progression along this line and have learned to dispense with a cartilaginous centre of ossification for the alisphenoid altogether.

Should it prove that this interpretation be the correct one, the designation "predeterminate" as applied to the prototherian bone is unfortunate in a genetic sense, "postdeterminate" would be more applicable. "There are more things in heaven and earth... than are dreamed of in our philosophy." Had I been endowed with *prévoyance* I should have selected a more purely descriptive designation for the alisphenoid not developed from its own specific centre of ossification.

Future investigation may demonstrate a pellicle of cartilage related to the tympanic wing, but it appears to be quite definitely established that the cranio-mural element of this peculiar alisphenoid is developed entirely in membrane (Watson, *l.c.* p. 323).

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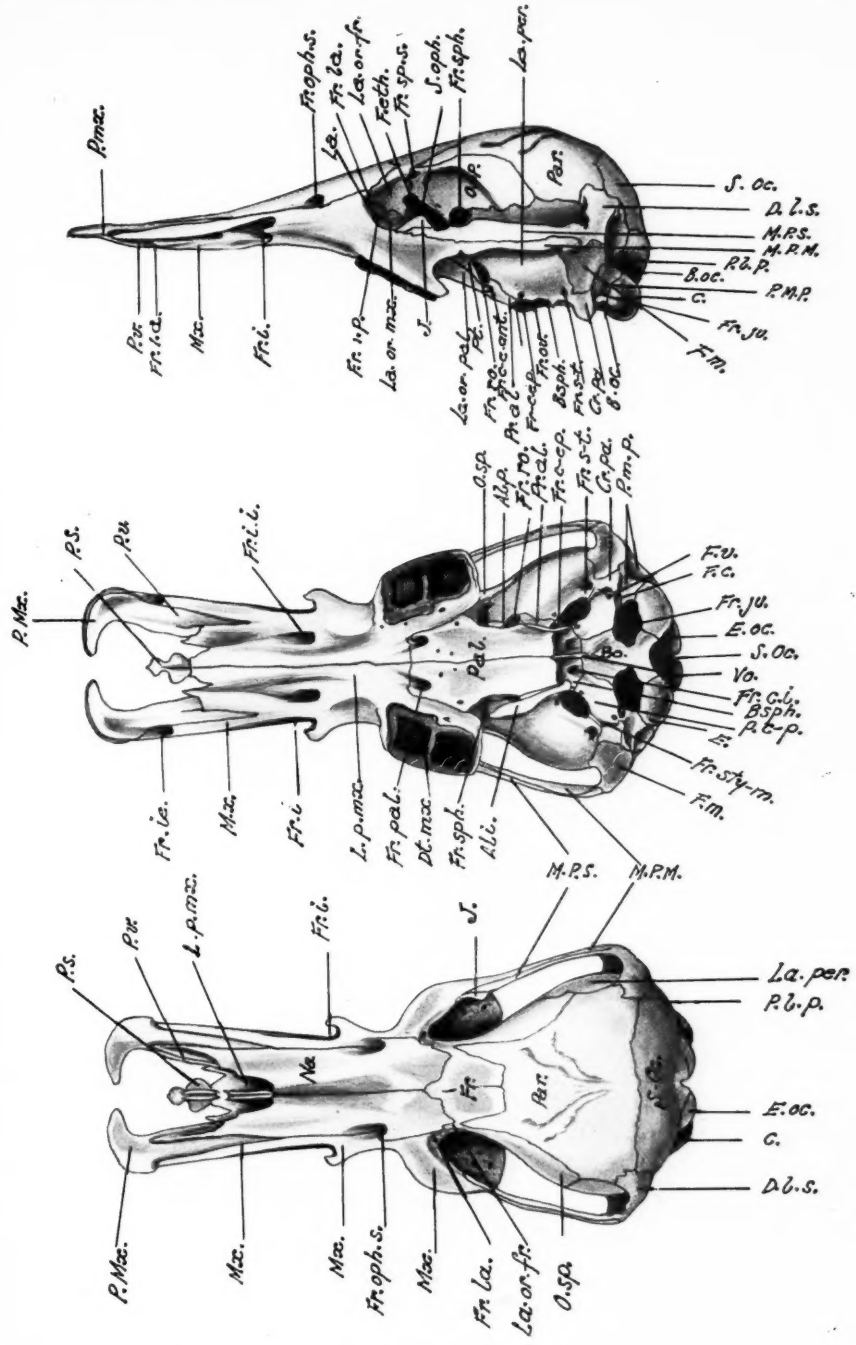
EXPLANATION OF THE ABBREVIATIONS USED IN THE FIGURES AND PLATE

A.l.e.	Margo anterior ossis ethmoidei.
Ali.	Ala tympanica ossis alisphenoidei.
A.l.p.	Processus antero-lateralis ossis basisphenoidei.
B.Oc. & *B.O.*	Os basioccipitale.
B.sph.	Os basisphenoideum.
C.	Condylus occipitalis.
Can.inf.	Canalis infraorbitalis.
Can.oph.	Canalis ophthalmicus.
Can.Vid.	Canalis Vidianus.
Cr.pa.	Crista parotica.
C.v.	Foramen vasculosum innominatum.
D.l.s.	Lamina dorsalis ossis squamosalis.
Dt.mx.	Fossa dentalis ossis maxillaris.
E.Oc. & *E.*	Os exoccipitale.
F.c.	Fenestra cochleae.
F.eth.	Fenestra ethmoidalis.
F.m.	Fossa glenoidea mandibularis.
Foss.fl.	Fossa arcuata (floccularis).
F.ov.	Foramen ovale.
Fr.	Os frontale.
Fr.c.-c.ant.	Foramen anterius canalis arteriae carotis externae.
Fr.c.-c.p.	Foramen posterius canalis arteriae carotis externae.
Fr.c.i.	Foramen arteriae carotis internae.
Fr.i.	Foramen infraorbitale.
Fr.i.a. & *Fr.ic.*	Foramen infraorbitale anterius.
Fr.i.i.	Foramen infraorbitale inferius,
Fr.i.p.	Foramen infraorbitale posterius.
Fr.ju. & *Fr.ja.*	Foramen jugulare.
Fr.la.	Foramen lachrymale.
Fr.oph. & *Fr.op.*	Foramen ophthalmicum.

Fr.oph.a.	Foramen ophthalmicum anterius.
Fr.oph.s.	Foramen ophthalmicum superius.
Fr.ov.	Foramen ovale.
Fr.pal.	Foramen palatinum.
Fr.pal.p. & *Fr.p.p.*	Foramen palatinum posterius.
Fr.ro.	Foramen rotundum.
Fr.sp. & *Fr.sph.*	Foramen sphenopticum.
Fr.sp.i.	Foramen sphenoidale inferius.
Fr.sp.s.	Foramen sphenoidale superius.
Fr.s.-t.	Foramen arteriae temporalis superficialis.
Fr.sty.-m.	Foramen stylomastoideum.
Fr.v.-c.l.	Foramen venae capitis lateralis.
Fr. VII	Foramen internum canalis Fallopii.
Fr. VIII	Meatus acusticus internus.
F.sp.	Fenestra sphenoidalis.
F.v.	Fenestra vestibuli.
G.mx.	Sulcus pro processo zygomatico ossis maxillaris.
H.l.	Hiatus Fallopii.
I.t.b.	Osses turbinata inferiores.
J.	Os jugulare.
La.	Os lachrymale.
La.or.fr.	Lamina orbitalis ossis frontalis.
La.or.mx.	Lamina orbitalis ossis maxillaris.
La.or.pal.	Lamina orbitalis ossis palatinis.
La.per.	Lamina alisphenoidea ossis periotici.
L.e.	Lamina nasalis (lateralis) ossis ethmoidei.
L.p.eth.	Processus lateralis ossis ethmoidei.
L.p.mx.	Lamina palatina ossis maxillaris.
M.p.m.	Processus zygomaticus ossis maxillaris.
M.p.s.	Processus zygomaticus ossis squamosalis.
M.t.b.	Os turbinatum medium.
Mx.	Os maxillare.
Na.	Os nasale.
O.l.	Lamina orbitalis.
O.sph. & *O.sp.*	Os orbitosphenoideum.
Pal.	Os palatinum.
Par.	Os parietale.
P.c.-p.	Pars cochlearis ossis periotici.
Per.	Os periotici.
P.i.e.	Postero-inferior lamina.
P.l.p.	Pars labyrinthinis ossis periotici.
P.m.p.	Pars mastoidea ossis periotici.
P.Mx.	Os premaxillare.
Pr.a.bsph.	Processus antero-lateralis ossis basisphenoidei.
Pr.al.	Processus alaris.
P.s.	Prevomer.
P.sp.	Os presphenoideum.
Pt.	Os pterygoideum.
P.t.c.	Canalis post-temporalis.
P.v.	Processus ventralis ossis premaxillaris.
S.	Sella turcica.
S.-f.-n.l.	Lamina subfronto-parietalis.
S.Oc.	Os supraoccipitale.
S.oph.	Sulcus ophthalmicus.
S.t.b.	Osses turbinata superiores.
Vo.	Vomer.



KESTEVEN AND FURST—THE SKULL OF *ORNITHORHYNCHUS*

POSTERIOR DUPLICITY IN A DOG, WITH REFERENCE TO MAMMALIAN TERATOLOGY IN GENERAL

By DONALD MAINLAND, M.B., Ch.B. (Edin.)
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In a valuable contribution to teratology, Stockard (1921) stated his belief that the only benefit to be derived from descriptions of isolated monsters was the aid which could possibly be obtained from them in studying the normal sequence of development. The admission of the embryological value of monsters in itself appears to justify the continued publication of reports on these specimens, and in fact necessitates considerable minuteness in the description of them. Moreover, although the large amount of recent experimental work on Fishes, Amphibia and Birds has led to a certain amount of agreement on the general nature of the mode of origin of monsters, there is still difference of opinion upon detail, nor is it by any means clear how far the knowledge obtained can be applied to Mammals. It is obvious that, unless some reasonably coherent theory of the mode of origin of the abnormal specimens be adopted, there will be little justification for an attempt to elucidate normal development by means of monstrosities; and it is equally obvious that, unless there is a considerable amount of information upon the normal development of the species, there can, as regards that species, be no adequate proof or disproof of any teratological theory. It is of interest, therefore, to ascertain in any given instance how far our present knowledge of development and our present views of teratogenesis elucidate each other. This is in part the object of the investigations recorded here, their primary aim being the description of an instance of posterior duplicity in a Mammal. This is a type of duplicity which appears less prominently in teratological literature than do some other forms, either because instances of it are less frequently met, or because, being less striking than anterior duplicities, instances of it are more frequently allowed to pass unrecorded. As will be mentioned later, however, this form of abnormality possesses features of special interest with regard to the mode of origin of duplicities in general.

The animal which forms the subject of the present communication was a newly-born French bulldog. Of the two other pups in the same litter both were unusually large, and one was born dead; no other gross abnormality was recorded in either[1].

[1] I am indebted to Dr Crew, Director of the Animal Breeding Research Department of Edinburgh University, for this specimen, and to A. D. Buchanan Smith, Esq., of that Department, for passing on to me the above information concerning its birth.

To Messrs Richard Burrell and W. F. Jenkins I am obliged for the drawing reproduced in fig. 5.

After injection of the arteries through the left ventricle of the heart with vermilion-urea-gelatine, the whole animal was preserved in formalin.

EXTERNAL APPEARANCE

The animal was photographed while fresh, and a drawing, prepared from the photograph, is shown in fig. 1. The part of the body on the cephalic side of the umbilicus showed no abnormalities. Four hind-limbs were present,

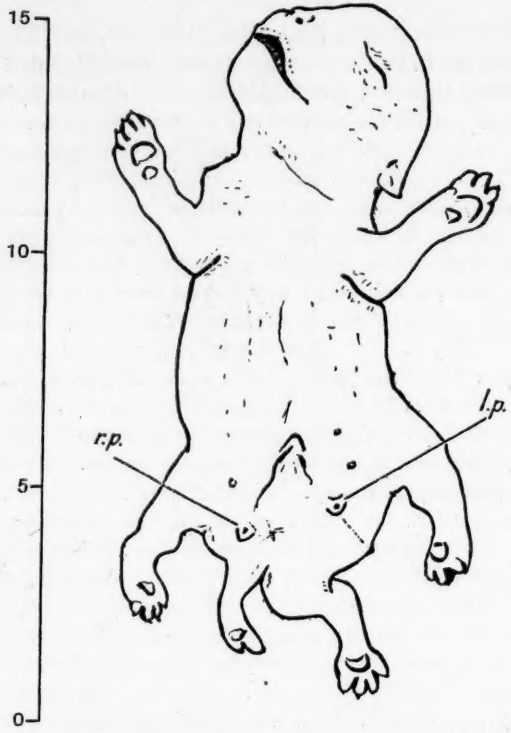

Fig. 1. (Drawn from a photograph; scale marked at intervals of 5 cm.)
r.p., right penis; *l.p.*, left penis.

which from their positions were designated right lateral, left lateral, right central and left central. In all four the segments, thigh, leg and foot, could be distinguished. The lateral hind-limbs were proportionate in size to the body and to the fore-limbs. The left central was slightly smaller than the left lateral, and the right central was thinner and shorter than any of the others, its length being approximately two-thirds of that of the left central. The two central limbs lay very close together at their roots. The right central hind-foot had

two digital pads, instead of the four possessed by the other hind-feet. One of these two pads was large, and this toe bore a double nail.

The umbilicus was single but occupied a broad area, from which a shallow pouch of peritoneum protruded. On the abdominal wall postero-lateral to the umbilicus on each side was a complete penis. Between the roots of the left pair of hind-limbs an anal orifice was situated, and dorsal to this was a tail of about one centimetre in length. There was no right anal orifice and no right tail.

OSSEOUS AND ARTICULATORY SYSTEMS

The numbers of vertebrae in the cervical, thoracic, lumbar and sacral regions were normal, as was also the number of ribs. There were only five

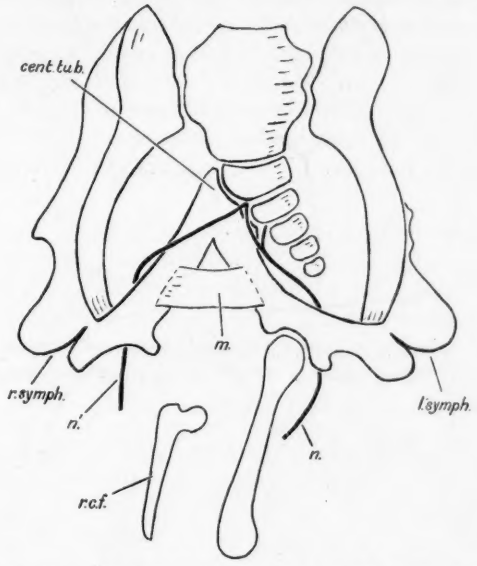

Fig. 2. Diagram of double pelvis from ventral aspect. *cent. tub.*, central tuberosity; *l. symph.*, left symphysis pubis; *r. symph.*, right symphysis pubis; *r.c.f.*, right central femur; *m.*, interpelvic membrane; *n.*, nerve to left central thigh; *n'.*, nerve to region at roots of right hind-limbs.

coccygeal vertebrae[1]. The tail was permanently pointed somewhat to the left, and the vertebrae composing it were shaped in conformity with this.

The bones and joints of the fore-limbs and skull were normal.

The sacrum articulated as in the normal with the iliac part of an os coxae

[1] No specific information on the number of coccygeal vertebrae in the French bulldog is available. For the dog in general, Ellenberger and Baum (*Anatomie des Hundes*, Berlin, 1891) give the variations as from 20 to 22.

on each side. The ventral parts of these laterally placed ossa coxae, instead of meeting in the mid-line, remained about 1½ cm. apart (fig. 2). Each articulated by its medial side with another bone, and thus two symphyses were formed, the long axes of which sloped dorsally and laterally. Each of the two extra bones (central ossa coxae) was rather more than half the length of one of the lateral ossa coxae, and each passed dorsally and medially, so that the two met and articulated with each other, slightly to the right of the mid-line. In the region of union the two bones formed a prominent tuberosity, which lay immediately to the right of and dorsal to the base of the tail. The first two coccygeal vertebrae articulated by their right sides with the left ventral portion of the tuberosity. The triangular interval between the central ossa coxae was partly filled by a strong quadrilateral membrane (the interpelvic membrane, fig. 2). About the middle of the medial surface of the left central os coxae was a small acetabular fossa, containing the head of the left central femur. The medial side of the right central os coxae presented a fossa which was deficient posteriorly, and contained loose connective tissue. The head of the right central femur lay a considerable distance to the left of this.

No obturator foramen was found on either of the central ossa coxae.

No abnormalities were found in the skeletons of the lateral hind-limbs.

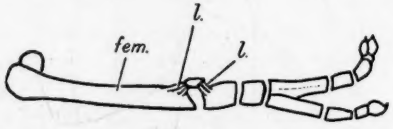

Fig. 3. Diagram of skeleton of right central limb from right ventral aspect. (The plantar surfaces of the foot bones are visible.) *fem.*, femur; *l*, *l*, ligaments attached to a structure resembling a patella.

The head of the right central femur lay in a hollow in the muscles of the right side of the left central thigh. The neck of the bone joined the shaft by passing to the right. Distally the shaft tapered, and articulated with a much shorter cylindrical cartilage by an oval facet facing distally and ventrally. The remaining skeletal parts are indicated in fig. 3. The extreme deformity of this limb rendered it difficult to determine whether the member corresponded in symmetry to a left or to a right normal limb. The body of the femur lay to the right of and distal to the head (fig. 2), but the plantar aspects of the metatarsals faced somewhat to the right as well as ventrally (fig. 3). The tarsal bones do not assist in the elucidation of this matter, and it is improbable that the small structure resembling a patella (fig. 3) was really such. On the whole the appearance of the limb suggested that it very probably corresponded to a right normal limb, that is, that it was of right "asymmetry."

The head of the left central femur articulated with the corresponding os coxae at the acetabulum. The distal end of the bone was broader than the shaft, but did not show definite condyles. With this end articulated a bone

comparable to a normal tibia. To the right of and ventral to this lay a flexible strip of bony or pre-osseous tissue which joined its neighbour proximally and distally, and apparently represented a fibula. If this interpretation is correct, then, as shown in fig. 4, the structure in question was placed abnormally in relation to the bones of the foot. The tarsals, metatarsals and phalanges were well defined and strictly comparable to those of a normal right foot.

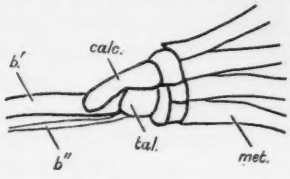

Fig. 4. Diagram of tarsus and adjoining parts in left central hind-limb from ventral aspect. (The plantar surfaces of the foot bones are visible.) *b′.*, principal bone of the leg (tibia); *b″.*, adjacent, fibula-like strip; *calc.*, calcaneus; *tal.*, talus; *met.*, metatarsal.

It may be concluded that this limb was a somewhat irregular limb of right "asymmetry." It was much more normal as regards skeletal parts than its neighbour on the right.

MUSCULAR SYSTEM

No abnormalities were noted in the muscles of the fore-limbs, head, neck or thorax.

A musculus praeputialis ran, laterally and caudally, to each penis. The oblique and transverse muscles of the abdomen were normal laterally. Those of the right side were widely separated from those of the left at the umbilicus, but posteriorly formed a continuous sheet, composed principally of obliquus internus and transversus abdominis. This sheet was attached to the bones of the right and left symphyses pubis, and to some extent to the membrane joining the two pelves. Each of the two recti abdominis was attached to the corresponding lateral os coxae, and for only a very short distance to the adjacent central pelvic bone. There was thus a considerable interval between these muscles in the pubic part of the abdominal wall. This interval was bridged by the aponeuroses of the lateral muscles of the abdominal wall.

The muscles of the lateral hind-limbs presented no abnormalities, and were easily defined. Those of the central limbs were more indefinite, and consisted of fibro-muscular masses more or less fused with each other. In the space between the two pelves, caudal to the interpelvic membrane, lay such a mass, with feeble attachments to bone.

In the left central limb, a thin layer of muscle passed from the mass just mentioned down the ventral aspect of the femur to the knee. This represented apparently the extensor muscle of the thigh. A better developed muscle passed from an attachment on the right of the left pubic symphysis to the dorsal aspect of the femur, and resembled an adductor. From the dorsal part of the central tuberosity (*cent. tub.*, fig. 2), and from the part of the os coxae which led from it to the left symphysis pubis, there arose a fairly well-defined muscle which was inserted partly into the dorsal aspect of the left central

femur and partly into bone of the leg distal to this. Except for this, muscular tissue in the leg was slight. In the sole of this limb was a fleshy mass subdivided to some extent, corresponding to the toes.

Muscular tissue in the right central thigh was poorly defined. Muscle which arose from the right side of the central tuberosity was inserted into the dorsal aspect of the femur, and muscle which arose from the left side of the right pelvis near the symphysis pubis lay on the right side of the femur. Practically all the muscle thinned out into fascia at the knee.

In these two central limbs, therefore, the degree of the abnormality of the muscular system corresponded closely to that of the osseous system. In so far as ordinary examination of the injected arteries allowed a conclusion to be formed, it appeared that poor development of the muscular tissue was not correlated with deficiency in the large vessels of supply to the limbs. It was observed that the definition of the muscles was greater where attachment to bone was possible.

ALIMENTARY SYSTEM

No reduplication of the alimentary canal or of its glands was observed in passing from the mouth posteriorly until the most caudal portion of the small intestine was reached. From the pylorus onwards the small intestine measured 38 cm. Four centimetres from its entrance into the colon, the small

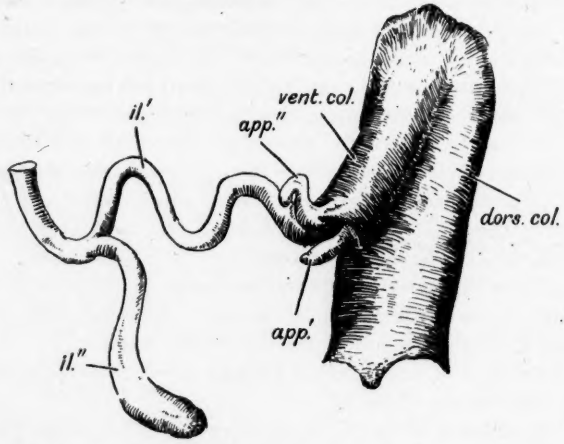

Fig. 5. Reduplicated part of intestine. *app'.*, *app".*, caecal appendices; *dors. col.*, dorsal limb of colon; *il'.*, ileum; *il".*, blindly ending branch of the ileum; *vent. col.*, ventral limb of colon.

intestine bifurcated (fig. 5). The narrower and thinner walled limb of the bifurcated part passed to the colon. The other limb, of equal length, lay beside the first, in a mesentery derived from the chief mesentery, and then ended blindly. The large intestine lay in the caudal part of the abdomen, to the left

of the median plane, and was shaped like an inverted U. The ventral limb of the U was about 1·5 cm. long. It received the small intestine, and presented two caecal appendices near the ileo-colic orifice. This limb was held by peritoneum to the surface of the dorsal limb, which was about 3·5 cm. long and was much distended by meconium. The terminal third of this dorsal limb bifurcated into a smaller, shallower right portion, which passed towards the right pelvic outlet, and a larger, deeper left branch, which passed towards the left pelvic outlet. The cavity of each branch was continuous with that of the corresponding urethra. The anal orifice present on the left side ventral to the root of the tail did not communicate with the intestine. On the right side there was no anal opening whatsoever.

Reduplication of the alimentary canal was therefore present in the distal part of the ileum, the caecum, and the terminal part of the rectum. The question might be raised whether the blind tube connected with the small intestine was a Meckel's diverticulum. Apart from the associated reduplicated caecum, two facts render this interpretation unlikely. One of these is the length of the tube, and the other is the presence of the remains of the vitelline arteries, which were found, as is usual in the newly-born Dog, at the umbilicus, quite unconnected with this tube.

UROGENITAL SYSTEM

There was both a right and a left bladder, each with a urachus. Each urethra communicated with the corresponding part of the divided rectum, the communication on the right side being much smaller than that on the left. The penile part of each urethra was patent. As the anus was not patent, the condition on both sides would be described as *atresia ani urethralis*. In the left lumbar region was a kidney, from which a ureter led to the left bladder. There was no kidney on the right, but a fine double cord-like structure attached to the right bladder near the base possibly represented the ureter of this side. The structure mentioned lay entirely in the pelvis, and the part of it remote from the bladder merely ended in fascia.

There was one testis in the lower lumbar region of each side. The epididymis of each was very imperfect. The two penes have already been noted. Each received a urethra through the corresponding pelvic outlet.

In the region between the two bladders, closely attached by peritoneum to the ventral surface of the rectum, was a lobulated gland-like structure, similar in size to each of the bladders. Caudally it was narrow and attached to the fascia of the pelvic floor. This structure and also one of the testes were examined histologically. Comparison was made with the testis of a normal pup removed from the uterus of a dog near the end of gestation. The lobulated structure in the pelvis of the six-legged dog was mostly composed of fibrous tissue, containing some small lymphocyte-like cells and some broad cells quadrilateral in outline. Identification either with post-natal or with foetal tissue was found to be impossible.

ARTERIAL SYSTEM

Before the body was preserved, the arteries were injected from the heart by a vermilion-urea-gelatine mass, and some of the finer points in the distribution of the limb arteries could be observed.

The abdominal aorta bifurcated opposite the posterior part of the lumbar region of the vertebral column. The two branches again divided, and contributed to the lateral hind-limbs arteries which corresponded in course and distribution to those of a normal animal. In addition, branches arose as indicated in the diagram (fig. 6). Among the arteries which resulted from the

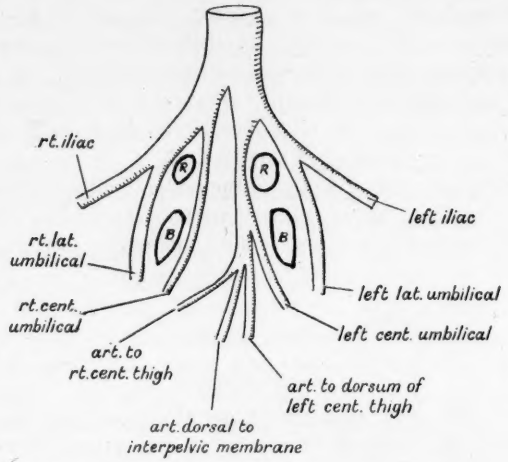

Fig 6. Diagram of posterior part of arterial system. *BB*, right and left bladders; *RR*, right and left subdivisions of rectum.

subdivision of the left terminal branch of the aorta were: (1) a left lateral umbilical; (2) a left central umbilical, which was smaller than the lateral, but adhered similarly to the left bladder; (3) arteries which emerged from the pelvis dorsal to the interpelvic membrane and supplied the fibro-muscular tissue between the two central limbs, and also the muscle of the left central limb which resembled an adductor; (4) a large artery which emerged from the left pelvic outlet, supplied the dorsal muscles of the left central thigh, and passed along the leg to the plantar aspect of the foot; (5) an artery which emerged through the right pelvic outlet and supplied the right central limb.

Among the branches of the right terminal division of the aorta were a right lateral umbilical and a smaller right central umbilical, both adherent to the right bladder.

It will be noted that both of the central hind-limbs were supplied by arteries which belonged to the left part of the double pelvis.

NERVOUS SYSTEM

The arch of the third sacral vertebra was thin and membranous. Distal to it was a small meningocele, which lay dorsal and to the left of the first two coccygeal vertebrae.

The nerve supply of both lateral hind limbs was normal. Dissection with the aid of a lens failed to reveal conclusively nerves to the central limbs except as mentioned below. A nerve emerged on the right side from between the first and second coccygeal vertebrae, and joined another which emerged, also on the right side, from between the second and third coccygeal vertebrae. The common trunk crossed the pelvic surface of the left central os coxae (fig. 2), and passed through the left pelvic outlet, to become the principal nerve of the left central limb. With the more cephalic root of this nerve lay another nerve, which emerged from the same intervertebral space, but left the pelvis through the right outlet, and supplied the skin of the region at the roots of the two right hind-limbs. No undoubted branches from it could be found supplying the muscles of the right central limb.

In contrast to the arterial supply of the central limbs, it is notable that the nerve supply of the left central and perhaps (indeed probably) that of the right central limbs originated in series with the spinal nerves of the right side of the body.

DISCUSSION

General scheme

The study of the mode of origin of any abnormality arising in embryonic life is necessarily based upon knowledge of the normal embryology of the species concerned; but in many groups of animals observation can be supplemented by experiment. At present a technique for the experimental production in Mammals of abnormalities such as that described here does not exist; and therefore comparison between the naturally produced and the artificially produced abnormality must entail reference to experiments on other groups of animals. It would not be profitable to discuss at length the various types of teratological experiments that have been performed, and the various theories that have been introduced to account for double monsters. Detailed information on these aspects of the subject is available in the work of Schwalbe (1907), and this can be supplemented from various subsequent papers, some of which contain useful bibliographical references (Anders, 1921 b; Stockard, 1921). Some twenty years ago, in spite of the numerous experiments that had even then been performed, Schwalbe (*loc. cit.*) felt that the only permissible generalisation was the limited one, that duplicities were due to the division of the material forming the egg, or, in the words of Rauber, that the germinal protoplasm was in such cases multi- instead of uni-centred. This statement referred to the "formal genesis" of duplicities (i.e. what might be called their mode of

origin). As regards their "causal genesis" (or actual cause), Schwalbe justly held that the existing knowledge was strictly nil.

At the present time it is sufficient to consider more recent views, which are based chiefly on experimental evidence, but which have themselves in part evolved out of the older knowledge and beliefs. An attempt can then be made to apply these views to the specimen described, to correlate them with the embryology of the Dog, and finally to seek further elucidation by brief reference to records of closely similar abnormalities.

Sources of embryological evidence

For a description of the early development of the Dog dependence has chiefly to be placed upon the work of Bonnet (1897, 1901). The numerous and carefully recorded observations of Bischoff (1845) afford considerable information, but they naturally do not afford evidence of minute differences in cellular activity or of the earliest stages of differentiation. Although the information is thus limited, sufficient is known to show that, as in other Mammals and in other non-mammalian Vertebrates, differentiation of the embryo proceeds first in a cephalo-caudal direction, and in particular that the hind-limb buds appear later than those of the fore-limb (Bischoff, 1845). Bonnet's records concern the stages from the formation of the embryonic area onwards. They are among the most minutely detailed of any in Mammalian embryology.

Experimental evidence

Within recent years extensive experimental investigations on the production of monstrosities have been carried out, especially in America, and some of the conclusions reached are of obvious importance to the present discussion, in which an attempt is made to apply the results of the experiments to another group of animals, Mammals, and to argue from these cases, where the causal agents were known, to a case where they are unknown. Thus, it appears now to be quite generally accepted: (1) that the type of the agent which causes the abnormality is a secondary matter, whether, for example, it is magnesium chloride, lowered temperature, or ultra-violet radiation (see Stockard, 1921; Marie Hinrichs, 1925; Bellamy, 1922); (2) that any one agent can produce a great many types of abnormality (see Stockard, 1921; Marie Hinrichs, 1925, 1927); and (3) that the resulting abnormalities reveal great similarity to each other among the various groups and species of animals.

A considerable amount of light has been thrown upon problems of teratogenesis by a number of authors who have applied to it Child's conception that during development the regions of high metabolism are regions of dominance which control the other regions. (For a concise critical statement of Child's position, especially regarding the cephalo-caudal metabolic gradient in Vertebrates, see a recent article by that author, Child, 1925. References to some of his previous publications are there given. A fuller bibliography is supplied by Conklin, 1924, p. 602.) As representative of investigations along

these lines mention may be made of the experiments of Bellamy (1922) on Frog embryos, and of Libbie Hyman (1921) on those of Teleost Fish. Although complete unity is not displayed in the conclusions reached by the various investigators, two main points of agreement may be stated as follows: (1) abnormalities arise because of the imperfect co-ordination between the parts with higher metabolism and the rest, as a result either of inhibition—an arrest of development (Stockard, 1921; Libbie Hyman, 1921; Bellamy, 1922)—or of acceleration (Riddle, 1923; Bellamy, 1922); (2) the parts most susceptible to interference by a teratogenetic agent are those of which the metabolic activity is highest, whether the interference causes the affected region to fail to regain its control of other regions (Stockard, 1921), or whether the activity of the susceptible region is directly accelerated (Bellamy, 1922), or whether the susceptible region shows more power of recovery than other regions (Libbie Hyman, 1921)[1].

Whatever be the ultimate destiny of the theory which has prompted these investigations, the value of their results is considerable, and, if these main points of agreement are accepted as at least the basis for a theory of teratogenesis, the mode of correlation of normal embryology with teratology is broadly indicated. It will not be permissible to assume that all the organs arising from a certain part of the embryo will be reduplicated or malformed. On the other hand it may be assumed that if regions or organs were in or about to enter a state of high metabolism when the teratogenetic factor became operative, then they will manifest abnormalities. Difficulty in the interpretation is, however, very liable to arise. At least four factors may be responsible for confusion and obscurity: (1) the possibility of the influence of several inhibiting or accelerating factors at different times; (2) the difference in susceptibility of the different germinal layers, shown experimentally by Libbie Hyman (1921); (3) secondary fusion of the parts of the embryo after primary separation (see reference to Fischel, below, and, especially as regards posterior duplicity, the reference to Hertwig in Schwalbe, 1907, pp. 60–1, also Marie Hinrichs, 1925); (4) the secondary changes which may occur during subsequent growth as a result of lack of room, alteration in blood supply or other factors (see Wilder, 1904). In the first instance, however, it is desirable to ignore these possibilities as far as possible, in order to test the validity of the conceptions mentioned, namely, that the causal agent operates in virtue of the susceptibility of the areas of high metabolism, and renders imperfect the co-ordination between these areas and the rest.

[1] Misconception may be avoided if it is stated that these references, which appear to suggest diversity of opinion, are intended to be representative, and not to be exhaustive either of the investigations or of the opinions held by the investigators named.

Period of origin of duplicities in general

Before these results of experiment are utilised in an attempt to determine in the present instance the time of operation of the teratogenetic factor, it is desirable to raise the question, within what period teratogenetic factors in general are supposed to act. Schwalbe (1907) stated as a widely accepted view the belief that gastrulation marked the end of the period during which most of the symmetrical duplicities were produced. This view has been reaffirmed more recently on experimental evidence (Stockard, 1921), and on morphological grounds (Lebedinsky, 1923), but individual specimens have been described which have been thought to demand a much later period of formation (Werber, 1917). Certain experiments (Kopsch, 1899; Baldwin, 1915; Marie Hinrichs, 1925) are of special interest because they demonstrate the possibility of production of posterior reduplications without anterior reduplication by interference with the ovum definitely before the embryonic area has formed. If this belief is accepted, as appears to be necessary, namely, that in most cases the teratogenetic agent operates not later than the gastrulation period or what corresponds to it in Mammals, and, further, if the assumption mentioned above of co-ordination and susceptibility be made, then our conception of the exact mode of action of the causal agent is more strictly defined. It is necessary to suppose that the effects of the agent will be manifested, not in virtue of incipient metabolic activity of various anlagen—for example, hind-limb buds—but on account of an earlier activity of the portions of the ovum destined to give rise to these anlagen.

Period of origin in this specimen

In the dog at present under discussion, it is noteworthy, firstly, that the abnormalities discovered were limited to the caudal part of the body, and, secondly, that, while the hind-limbs and pelvis were multiple, the tail was rudimentary. The vascularity of the parts about the pelvic outlet was considerable, and there appeared no reason to suppose that the tail, if able to demand greater nutrition, would have failed to receive it. More probably, the activity of the elements forming it was in the first instance depressed, and never completely recovered. The restriction of the abnormalities to the caudal portion of the body renders this and other cases of posterior duplicity of special interest in connection with the beliefs that high metabolism accounts for susceptibility to the causal agent, and that this agent does not act after the gastrulation period (or what corresponds to it in Mammals). After the gastrulation period, when the embryonic area becomes trilaminar, the region of high activity is in the future cephalic part. Therefore, where the ultimate reduplication is, as in the specimen described, purely posterior, it must be supposed either that secondary changes have taken place, or that the effect of the causal agent was not originally uniform on all parts of the ovum or gastrula. In accordance with the views of co-ordination and susceptibility stated above,

it may in this case be suggested that the agent, whatever it was, affected the ovum during a period of activity of the parts destined, at a later stage, to give rise to hind-limbs, alimentary tract, bladder and urachus; the effects being the prevention of the normal co-ordination in development with consequent reduplication of parts on opposite sides of the future median plane.

From the experimental evidence referred to, it appears quite reasonable to ascribe the deficiency of the tail to the same factor, which in this instance exerted a purely depressing effect. The defective and deformed structure of the central hind-limbs may be accounted for by restricted room (Wilder, 1904), or by deficiencies in the anlagen, induced at the time of reduplication.

In an attempt to correlate in further detail the course of development in the normal with the abnormal occurrences in this animal, appeal may be made to the facts of comparative Mammalian embryology, but here care must be exercised, owing to the known divergence in detail between the development in various species. For this purpose reference will be made to the embryology of Man and of the Pig, both of which have been studied attentively. Bischoff's (1845) records show that in the Dog the tongue manifests early activity after the appearance of the hind-limb buds, but apparently before the genital tubercle arises. That this is not an exceptional sequence is shown by records concerning Man (Keibel, 1910, pp. 68–9—hind-limb; McMurrich, 1912, pp. 343–4—tongue; Felix, 1912, p. 947—genital tubercle) and the Pig (Arey, 1925, p. 355—hind-limbs; *ibid.*, fig. 84, p. 95—tongue; *ibid.*, p. 378; and Bühler, 1906, fig. 495, p. 840—genital tubercle). In the specimen examined there was reduplication of the hind-limbs and of the external genitals, but there was no obvious abnormality of the tongue. Visible development of an organ is only a late result of metabolic activity, and therefore the weakness of the embryological evidence is readily admitted; but the line of argument indicated is definite. If the facts are as stated, a period of high metabolism in an anlage that apparently was not affected intervened between the high metabolic periods of two anlagen that were reduplicated. The reduplication of organs appears to be determined by their situation, not by their known metabolic history. If the causal agent was single and yet acted on parts in virtue of their high metabolism, then it is suggested either that a specially localised fusion of certain reduplicated organs took place, or, as is less hypothetical, that the cause operated before differentiation had proceeded far, and that at some period the cells destined to give rise to the caudal part of the embryo were highly active, while the rest were not. This view, supplemented by the fact of the high primary cephalic activity mentioned above, would indicate that the causal agent was effective at a period before the trilaminar stage of the embryonic area. The result of this argument would be to show that the assumptions of co-ordination and susceptibility made above, when applied to a case of posterior duplicity, practically pointed to the general conclusion already stated, that such abnormalities do not arise after the gastrulation stage or what corresponds to it in Mammals (p. 484).

Even Bonnet's (1897) minute embryological observations do not justify any more strict definition of the time of origin.

As the lobulated fibro-cellular mass in the pelvis of this dog was not identified, it is hardly justifiable to make any assumption that would exclude the possibility of its being either nephrogenic or genital tissue. This difficulty affords an instance of an essential weakness in teratological records based upon ordinary dissection and naked-eye observation, and this weakness is not always overcome by histological methods, such as were used in the present case. Evidence of the absence of reduplication of any organ or tissue may be untrustworthy because an originally doubled portion may have regressed so far as not to be readily recognisable (Stockard, 1921), or even so far as to be undetectable. This source of error can be removed probably only by a graded series of strictly controlled experiments (not necessarily on Mammals), followed by a histological examination of the products.

If, however, it was assumed that the testes in this specimen were unreduplicated, and if the assumption was supported by reference to Horsley's specimen (see below, p. 491), the line of argument from embryology would be the same as in the case of the tongue, the sequence of appearance being, according to evidence from Bischoff (1845), hind-limb buds, genital glands, genital tubercle. (Compare Man—references to hind-limbs and tubercle as above; genital gland: Felix, 1912, p. 885.)

The earliest time of action of the cause

In the search for evidence of the earliest activity of the causal agent in this specimen, attention may be turned to the urachus. Reduplication of this structure as far as the umbilicus has been noted. In the Dog, Bonnet (1901) detected cellular changes in the entoderm of the future allantoic region before any mesodermal somites had appeared, and he stated that in embryos with from eight to ten somites this allantoic entoderm was for the most part very clear. Differentiation in this part, therefore, arises before the appearance of either the buds of the fore-limbs, which were not reduplicated here, or of the buds of the hind-limbs, which were reduplicated. Even if it be assumed that the agent responsible for the reduplication was effective only during high metabolic activity of the parts concerned, it is, on this evidence alone, impossible to state whether the agent operated at the period when the urachus commenced to differentiate, or during its period of high metabolic activity immediately subsequent to that (Bischoff, 1845), or at a much earlier period in the history of the developing zygote.

Although the first incidence of the teratological change on this specimen cannot be more nearly determined than has been stated, it has been found (e.g. by Marie Hinrichs, 1925, experimenting on Fishes) that reduplication, including posterior reduplication, can occur when ova are subjected to the teratogenetic agent within the first few minutes of fertilisation. Attempts to account for this may take one of several forms. Very early physiological or

constitutional differences in the zygote were suggested by Marie Hinrichs herself. It would be unprofitable to enter into a discussion of the differentiation of the unsegmented Mammalian ovum in connection with the present specimen; but this explanation cannot on that account be rejected. To adopt the theory advocated at some length by Fischel (see Schwalbe, 1907, and Werber, 1917), namely, complete separation of the ovum into two followed by partial reunion, would be to introduce an additional assumption to those already made; and there appears to be as much evidence in support of a suggestion based on the assumptions of co-ordination and dominance. It might be supposed that the effect of the interference with the ovum was to produce a greater or lesser degree of inco-ordination, and that at the first differentiation the part which usually dominated and controlled the growth of the rest had to some extent lost this power, the degree and even the type of the deformity depending on the extent of the loss, both in the case of the part which should dominate first, and of the parts which should dominate later.

The alimentary system

Reduplication of the alimentary system of this specimen has been noted as confined to the caudal portion of the small intestine, the caecal region, and the terminal part of the large intestine. The part affected, therefore, appears to be wholly or almost wholly caudal to the position of the vitello-intestinal duct. While it is known that, during the developmental activity of the tail region of the embryo, all the germinal layers are more or less involved, detailed knowledge of the metabolic relationships is still small. Moreover, in experiments to test the metabolic activity of developing ova by toxic solutions, entodermal structures frequently cannot be studied (Libbie Hyman, 1921). It is therefore impossible even to attempt to decide whether the incompleteness of the reduplication of the large gut was due to a secondary fusion, or to a primary difference in the metabolic activity of the cells which were destined to form it. Variations in the extent of doubling of the intestine in cases of posterior duplicity are considerable, as may be seen by comparing the present case with those of Anders (1928, p. 421), Sara Conrow (1917), and Horsley (1920).

Fission and hyper-regeneration

Schwalbe (1907, p. 306) remarked, in connection with a case of posterior duplicity in a dog described by Otto, that the absence of reduplication of the vertebrae rendered it doubtful whether the specimen ought to be considered a true posterior duplicity or a product of fission of the pelvis with subsequent hyper-regeneration, such as was produced by the experiments of Tornier on Amphibia. In these experiments (Tornier, 1906) the hind-limb buds were cut through, and the results, carefully described and illustrated, afford a basis for comparison with naturally occurring duplicities of the pelvic region. In the possession of an unreduplicated vertebral column the present case resembles that of Otto, and, moreover, Schwalbe's remark raises the important question

of the relationship between experimentally produced accessory limbs and cases of duplicity occurring in nature. Since Tornier's work a large amount of research has been carried out on the regeneration and other changes resulting from the splitting, excision and transplantation of limb-buds (Harrison, 1921; Spurling, 1923; Swett, 1924; etc.). Much attention has been paid to the question of symmetry. If redundant limbs in any natural specimen are to be regarded as the products solely of such a process of fission and hyper-regeneration, then the rules of symmetry demonstrated by experiments of that kind would necessarily be assumed to act in such a specimen also. Swett (1924) gives a summary of the conclusions justifiably drawn from his own investigations and those of others, to the effects: (1) that both primary limbs developing from isolated portions of a limb-bud always exhibit the same "asymmetry" (both being left limbs or both right); (2) that a secondary limb formed by budding is a mirror image of the primary (in accordance with Bateson's rule of minor symmetry); (3) that, however, the boundary line between these two methods of double limb formation is very indistinct. That unity upon this question is not reached is indicated by the article of Lataste (1926). The great extent of the question and the value of analogies obtained in remote fields may be illustrated by the investigations of Goldschmidt (1921) on naturally occurring reduplications of the copulation apparatus of the gipsy moth (*Lymantria dispar*). The conclusions from a study of symmetry are that fission and budding occur in these cases.

Swett's immediate purpose in the paper just referred to (Swett, 1924) was the discussion of exceptions to Bateson's rules of minor symmetry, and in the course of it he expressed the belief that many cases of extra limbs recorded among the higher Vertebrates, including Man, are exceptions to these rules. Instead of two adjacent members in sets of double or multiple limbs forming a mirror image of each other in accordance with the rule, limbs of the same "asymmetry" may lie side by side—two right limbs or two left limbs may be adjacent. There is no detailed treatment in his paper of the examples in higher Vertebrates.

If it becomes possible to subdivide duplicities of limbs into those which present the mirror image relationship and those which do not, the results may have some etiological importance, but will not necessarily prove Schwalbe's (*loc. cit.*) suggestion correct. One of the chief obstacles to such a classification is emphasised by Lataste (1926), and is illustrated by the present specimen—the difficulty of determining the symmetry of the limbs. The left central hind-limb in the dog described was a (slightly irregular) right limb, and therefore a mirror image of its left lateral neighbour; but the true "asymmetry" of the right central hind-limb is still somewhat in doubt. If it was of right "asymmetry," which appeared to be very probable, then the sequence of hind-limbs is, from left to right: LRRR. The difficulty in deciding this question is partly due to the extreme deformity of the limb; but it is possible that it may be to some extent due to an incomplete process of rotation of developing limbs,

by which Swett (1924) accounts in part for the exceptions to the rule of mirror images.

Even if it should be shown that cases such as the present are due to such a process of "fission" of a limb-bud with hyper-regeneration, it might well be that the fission was simply a physiological isolation of parts, a conception quite closely akin to that adopted above as the basis of this discussion, namely a lack of co-ordination. If such an explanation were adopted in regard to the dog described here, it would imply that from one limb-bud three limbs developed; from the other, only one limb. It might be expected that the nerves supplying or associated with the limbs would afford a clue to the side of the embryo from which the limbs arose, and therefore that the right lateral and both central limbs of this specimen were products of the right hind-limb bud. It might, however, reasonably be supposed that the products of fission or reduplication acted as a transplant in such experiments as those of Detwiler (1924), and became supplied by nerves from parts of the cord not normally supplying limbs at all. The only nerves supplying or associated with the central limbs in this specimen actually made their appearance in series with the nerves to the right lateral hind-limb, but more caudally.

The chief arguments against the suggestion of fission of the limb-bud in this specimen are, firstly, the extent of the abnormalities (involving alimentary system, urogenital system and the coccygeal part of the vertebral column), and, secondly, the probability indicated above that the time of operation of the cause must be referred to an earlier period in the ontogeny of the specimen than the period of limb-bud formation.

Minor accompanying abnormalities

It may be asked whether the other abnormalities recorded in this dog (meningocele, *atresia ani urethralis*, unilateral absence of a kidney) can be accounted for in such a way as to harmonise with the principal lesions. The cause of the defective tail may well have been the cause also of the imperfect formation of the vertebral canal; but to ascribe directly to the same cause the imperfect development of the uro-rectal septum would hardly be more than a conjecture. It is an interesting coincidence that in both of the recently recorded specimens of posterior duplicity mentioned below, there were kidney defects. In Horsley's specimen (1920) there was only one kidney; in Sara Conrow's (1917) one of the two kidneys was rudimentary.

With regard to the *atresia ani*, one may recall the recent work of Anders (1921 a), who came to the conclusion that where the hind-gut opened into the cloaca or ended blindly high up in the pelvis, the ectodermal depression or anus was absent. This was attributed to the fact that the distance between the entoderm and the ectoderm prevented a chemotactic action of the former. In the dog described above it is interesting to note that the larger, left branch of the rectum, which penetrated more deeply into the pelvis, corresponded to the single anal depression. There was, however, no very great difference

in depth between the two blind ends of the rectum, and if the theory of chemotaxis be assumed, then the absence of a second anus is perhaps more adequately explained by the lesser degree of activity of the right half of the rectum.

Differences between components

The great variation in the degree of similarity between the two components of double monsters is at once striking. The dog here discussed is, comparatively, symmetrical, but is not quite so. It is not possible to do anything more than surmise the cause of these differences; but their existence becomes important in connection with the more completely reduplicated human monsters such as the Siamese Twins. A short time ago, Regnault (1925) remarked upon the great differences, physical and psychological, between the two components of such double human monsters, and pointed out how, by excluding the effects of heredity, of the external environment, and of the vascular factor in the internal environment (all of which were common to both components), it was possible to attribute certain phenomena definitely to the nervous factor in the internal environment. Among these were hunger, sleep and the menstrual flow. From brief consideration of minor differences, such as those present in the dog described, where there is only one nervous system, it is obvious that at a very early period of development differences arose in the structure and obviously in the future function of the component parts. Differences of this fundamental kind, but varying in degree and involving other organs and other functions, obviously exist in the more nearly complete duplicities. Therefore, whatever will ultimately be found responsible for these differences, it is impossible to use them as a proof of certain functions of the nervous system.

Other cases of posterior duplicity

For comparison with the specimen described above, brief reference may be made to several other instances of posterior duplicity in Mammals. Concerning the instances which have occurred in the human species little more is known than the peculiarities of external form. Records of these may be found in the writings of Wilder (1904, 1908), Schwalbe (1907) and Broman (1911). As regards the non-human Mammals[1], reference has already been made to the example quoted from Otto by Schwalbe (1907) (a female dog, single from head to umbilicus, with single vertebral column, single left anus, double pelvis, four hind-limbs, double vulva, double caecum, small gut apparently for the most part single). Two instances of animals, each with six hind-legs, are a male rat described by Sara Conrow (1917) and a female dog described by Horsley (1920). The latter case, occurring in a dog, is of special value for comparison with the bulldog pup described above. In both of these

[1] Schlegel (1921) has published a series of short abstracts of many of the cases of monsters (chiefly non-human) described in the first two decades of this century. His article forms, therefore, a valuable supplement to the earlier volumes of Schwalbe's *Die Morphologie der Missbildungen des Menschen und der Tiere.*

last-mentioned dogs the reduplication affected the pelvic girdle, the external genitalia and urinary bladder; the genital glands were apparently unreduplicated. In Horsley's specimen, however, the vertebral column was apparently doubled in the sacral region; whereas in the bulldog described here this was not so. On the other hand, in the latter specimen reduplication extended into the caudal part of the small intestine; in Horsley's dog it was restricted to the large bowel. If it be supposed that rates of metabolic activity in the different parts of the ovum are the primary factors in determining the distribution of the abnormalities, the question arises whether the normal sequence of embryonic development would account for these differences. In the rat described by Sara Conrow (1917) the vertebral column was single throughout, and there were two pelves and two penes as in the bulldog described here; but in the rat there were four testes, while the urinary bladder was incompletely doubled, and, although there were two ani (one a false one), the alimentary canal was otherwise little affected. When this specimen is compared with the dog described by Horsley and with the bulldog pup described here, it may appear questionable whether the differences in times of development between the two species, or between individuals of the same species, are sufficient in themselves to account for the differences in distribution of the duplicities. It may be suggested that some process of secondary fusion of parts, or of absorption of reduplicates, or some specific difference in the causal agents, must be postulated. While it cannot be denied that some or all of these factors may be operative, it may still be possible to account for the differences in the results solely by differences in the state of metabolism of cells or cell-masses in the developing zygote, the causal agent being assumed to act only on the more susceptible, that is, the more active cells or masses. It is known, in general, how cells and cell groups of a zygote can pass rapidly from a state of activity to one of quiescence, and how one mass may be active and a neighbouring mass apparently inactive; but to show in detail the normal sequence of these changes in Mammalian ova by modern cytological, especially cytoplasmic, technique, is a task for the future.

Future investigation

In the preceding discussion there have been shown some of the problems that arise and the difficulties that are encountered when an attempt is made to correlate an instance of reduplication in a Mammal with the results of the more recent teratological experiments on other groups of animals. It is obvious how few justifiable inferences can be made from such a comparison. Lack of embryological information may appear to render the Dog a rather unfortunate species for this type of investigation; but it is very questionable whether the existing embryological knowledge concerning any Mammal is sufficiently detailed as regards the cytological changes to afford satisfactory evidence on the point at issue, namely, the normal sequence of metabolic activity from the stage of fertilisation onwards. On the other hand, experiments on other groups

do not yet afford sufficient information to enable descriptive teratology to contribute to the question of cell-lineage in Mammals, as, sooner or later, it probably will do.

It may, perhaps, not be out of place to consider briefly certain points with regard to the future of Mammalian teratology. Such advanced degrees of abnormality as the one here described are, of course, comparatively rare, perhaps so rare in human development that their causation may be held of little moment. There appears, however, no justification for the supposition that they are, causally, at all widely removed from many of the minor abnormalities which are more common and of which some have practical importance in human medicine. From the purely biological standpoint, and therefore ultimately also from the medical standpoint, the importance of all these abnormalities in all species of animals becomes greater as the purely mechanical theories of their causation become less plausible.

In most groups of animals the determination of possible causes and of the mode of production of abnormalities can be facilitated by experiment; and there is even the danger that repeated observations of natural specimens and of the normal development may be neglected. In Mammals, while attempts at experimental production should be carried out, the careful dissection and histological examination of natural specimens is of the first importance. It is, however, obviously undesirable that space in anatomical journals should be frequently occupied by such detailed descriptions, which have their chief value as part of a large series. It is perhaps desirable that the instances studied should be restricted at first to one species, of which the early development was known in great detail by the investigators. The rarity of certain forms of terata might, however, render it necessary that more than one species of animal be included. Throughout the investigations correlation with recent experimental work should be attempted. Minute examination, both histological and biochemical, of the mother of the abnormal specimen should be made. To insure the possibility of this, research would probably have to be restricted to animals bred in large numbers for research. These lines of approach all seem necessary if light is to be thrown, not only upon the mode of origin of these abnormalities in Mammals, but upon the very obscure question of their actual cause.

SUMMARY

The specimen was a French bulldog, newly born.

Externally it was reduplicated only caudal to the umbilicus.

There were two pelves, two normal lateral hind-limbs, and two centrally placed hind-limbs. The left central hind-limb was more nearly normal than the right central, in osseous and muscular structure, and corresponded in symmetry to a normal right limb. The right central limb was small and de-

formed. It was of doubtful symmetry, but probably also corresponded to a normal right limb.

The rest of the skeleton was not reduplicated. The coccyx was very short and deformed. The abdominal muscles were only slightly abnormal. The arteries supplying both central hind-limbs came from the vessels in the left pelvis. There were four umbilical arteries.

Only two nerves could definitely be shown to be associated with the central hind-limbs: one to the left central, and one to the skin at the root of the right central limb. These nerves appeared in series with the lumbar and sacral nerves supplying the right lateral hind-limb; but were more caudal than these, for they corresponded to coccygeal nerves.

In the alimentary system the reduplications affected only the terminal one-tenth of the small intestine, the caecum (two caecal appendices), and the rectum. There was only one anus. It corresponded to the left branch of the rectum, and was imperforate.

There was only one kidney. It was present on the left side. There were two urinary bladders, each with a urachus. Each urethra communicated with the corresponding part of the divided rectum.

There were two penes; but only two definite testes were found. Between the urinary bladders and the colon lay a fibro-cellular structure, covered with peritoneum. It was not identified.

Facts are mentioned which support the application to a mammalian monstrosity of the results of experiments employing known causal agents upon non-mammalian animals (p. 483). The assumptions based on these experiments (mostly recent) are: (1) that abnormalities arise because of imperfect co-ordination in the developing zygote between parts of high metabolic activity and the other parts; and (2) that these highly active parts are most susceptible to the causal agents.

The sources of information upon the early embryology of the Dog are not numerous; but the general scheme of development is known, and, concerning certain aspects, a considerable amount of minute detail is available.

Posterior reduplications are of special interest in view of the assumptions of co-ordination and susceptibility, because, after the trilaminar stage of the embryonic area has arisen, metabolic activity is highest first in the future cephalic region. To this fact is added the observation that, in the specimen described, parts (tongue and perhaps testis) apparently unaffected by the teratogenetic agent, had, so far as available embryological evidence shows, a period of high initial activity in the interval between the periods of activity of organs or anlagen here reduplicated (hind-limbs, genital tubercle). The conclusion indicated is that, on the assumptions made, the cause, if single, operated at some time when all the future caudal parts of the embryo were active, and the rest were not, i.e. before the trilaminar stage. This is in agreement with the widely held belief that gastrulation (or what corresponds to it in Mammals) is the latest period of origin of symmetrical duplicities.

More definite determination of the time of action of the cause was impossible; but experiments on other groups of animals show that this period may be immediately after fertilisation.

Reduplication in the alimentary system apparently was confined wholly or almost wholly to the part caudal to the vitello-intestinal duct.

Lack of evidence of reduplication may vitiate any teratological record such as the present one, because reduplicated parts may have regressed. Histological methods are not always sufficient to obviate this difficulty, which can probably only be overcome by experiment.

Even although the vertebral column was not reduplicated here, it is improbable that, as Schwalbe (1907) suggested, fission and hyper-regeneration of a limb-bud would account for this type of abnormality. Relations of symmetry between limbs are important in this connection. A common source of difficulty in the determination of the symmetry of a limb is illustrated by the deformed right central hind-limb of this specimen.

Differences between the components of double monsters are fundamental, whatever their origin. Those present here, where the nervous system was single, are comparable with those between the two components of more nearly complete double monsters, with separate nervous systems. Therefore the latter do not, as Regnault (1925) has suggested, enable one to ascribe certain functions to the nervous system.

The differences in distribution of reduplications between the various cases of posterior duplicity are considerable. They may have to be accounted for by some factor other than the primary cause acting as assumed here; but it may well be that minute metabolic differences in the developing zygote are sufficient. Knowledge of this detail is yet inadequate.

Reasons for the continued study of such Mammalian monsters are indicated, and methods of systematic investigation are suggested.

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WINNIPEG,
6th *June*, 1928.

ANATOMICAL NOTE

VENAE CAVAE SUPERIORES DEXTRA ET SINISTRA OF EQUAL SIZE IN AN ADULT

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THE cases of persistent left superior vena cava described in the literature have not yet attained such numbers that the recording of additional cases lacks significance. This opinion is strengthened by the diversity of the vascular conditions exhibited by the various specimens; for example, in some cases the left superior vena cava persists alone, whilst in others both right and left vessels are present; specimens in the latter group exhibit very striking variations in the size of the two vessels. Attempts to analyse the factors underlying the morphogenesis of these vessels cannot be deemed adequate unless and until all the known variations are understood. In other words, the recording of such cases assists our comprehension of the problem requiring solution.

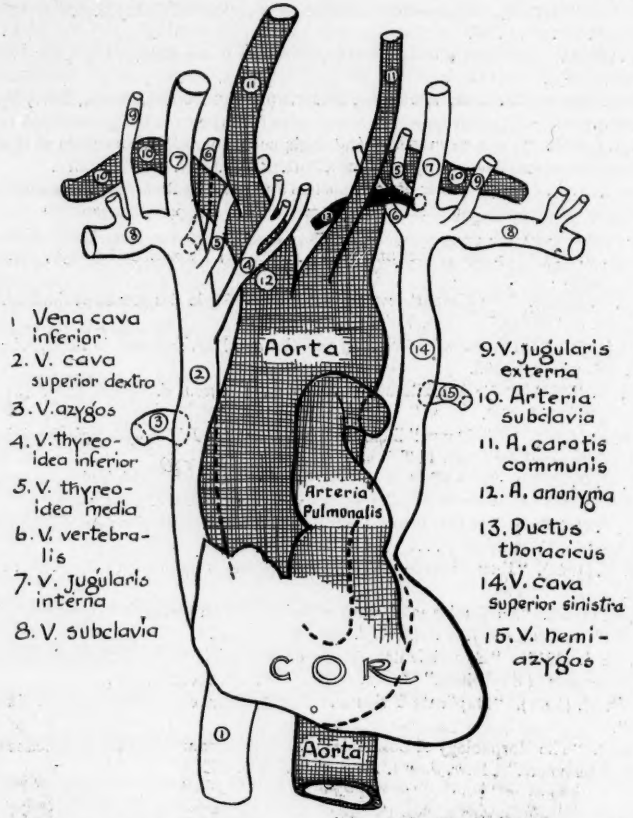

Fig. 1. Sketch from the ventral aspect, showing right and left superior venae cavae and their tributaries.

The present case is that of a white male, *aet.* 55, a labourer by occupation, the cause of whose death was certified as diabetes mellitus; nothing further is known concerning him.

The anatomical arrangement is indicated in the accompanying sketch, for which the author thanks Mr M. G. Chepourkoff.

The heart is relatively small; this feature is slightly exaggerated in the drawing, however. A well-developed superior vena cava is present on each side, commencing by the union of the internal jugular and subclavian veins. The equality in calibre exhibited by the two vessels is striking.

The right superior vena cava enters the right atrium in the usual manner, as does the inferior vena cava.

The left superior vena cava descends on the left side of the aortic arch and in front of the root of the left lung, then dorsal to the left auricle and atrium to the region of the atrioventricular sulcus where, slightly dilated, it proceeds towards the right to enter the right atrium. This latter part of its course, corresponding to the coronary sinus, is indicated by dotted lines in the diagram, which is drawn from the ventral aspect.

In addition to the right internal jugular and subclavian veins, the right superior vena cava receives (1) the inferior thyreoid veins; (2) another vein from the thyreoid gland, evidently the right middle thyreoid vein; (3) the right vertebral vein; (4) the vena azygos.

In addition to the left internal jugular and subclavian veins, the left superior vena cava receives (1) the thoracic duct, which empties into its commencement, in conjunction with (2) the left middle thyreoid vein; (3) the left vertebral vein; (4) the hemiazygos vein (there is but one); (5) veins from the heart.

There is no anastomosing vessel joining the two superior venae cavae, nor any other noteworthy anomaly.

This is the second left superior vena cava seen by the writer. The other, observed a year or two ago at McGill University, Montreal, was likewise in an adult, but differed from the present specimen in that the right superior vena cava was a diminutive vessel and the right innominate vein crossed to empty into the left superior vena cava, the condition approaching, but not attaining, the complete mirror-imaging described by Halpert.

Persistent left superior vena cava has been the subject of a considerable number of publications, a few of the more recent of which are listed below. Odgers and Harris give references which will guide those interested to the literature. The morphogenesis of such cases is discussed briefly by Harris and his collaborators and by Hurley and Coates; likewise, of course, by many of the older writers.

The present case is recorded because it belongs to the minority observed in adult subjects and because of the unusual equality in size exhibited by the two superior venae cavae.

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REVIEWS

Beitrag zur Kenntnis der Klinischen Verwertbarkeit des Holmgrenschen Frontalreflexes. [*Contribution to the clinical application of the Frontal Reflex of Holmgren.*] By ALBERT GRÖNBERG. Acta Medica Scandinavia, Supplementum XXV. Stockholm, 1928.

The author records 300 clinical cases in which the reflex was studied. The protocol for each patient is rich in clinical detail and the numerous illustrations of the brain sections at autopsy afford material of great value to the study of other problems. The frontal reflex of Holmgren is elicited as follows: Slight pressure or pinching, or even touching, of the skin in the frontal region leads to wrinkling of the skin of the forehead, and lifting of the eyebrows on both sides. This is the classical reflex. More frequently the eyebrow is raised on the one side only, or, more rarely, on the opposite side. A hot or cold stimulus to the forehead may also elicit the reflex. The contraction of the brow persists for several seconds.

The conclusions are:

(1) Pseudo-frontal reflexes or true frontal reflexes may arise in non-cerebral disease.

(2) A positive or negative frontal reflex does not appear to be associated with any specific neurological symptom complex.

(3) Aphasia seems to be more frequently associated with a positive reflex, and also those tremors of the type which occur in the extra-pyramidal symptoms complex.

(4) The frontal reflex behaves in the same manner as other superficial reflexes in states of coma and somnolence.

(5) The frontal reflex is usually negative in the first 24 hours of cerebral disease and in those acute cases where death occurs within 48 hours.

(6) The frontal reflex may occur in general intoxications without local lesions, and in cerebral lesions which affect either the cortex, the meninges, the basal ganglia or the cortex and basal ganglia jointly.

(7) No localisation of a lesion which would lead to a positive frontal reflex could be made.

Thus the frontal reflex has but little clinical significance as compared with the Babinski extensor response and the superficial abdominal reflex. It belongs rather to such a group as includes Chvostek's sign.

Handbuch der Anatomie des Kindes. Erster Band, 2. Lieferung. Topographische Anatomie und äussere Gestalt. By WILHELM PFUHL, Greifswald. Brustorgane des Kindes. By LUDWIG GRAPER, Jena. (Munich; Bergmann.) 1928. Pp. iv + 191–320. 51 Figs. and 30 Tables. Price 18 gold marks.

The second part of the first volume of this Handbook to the Anatomy of the Child, by Profs. Peter, Wetzel and Heiderich, contains a comprehensive survey of the present state of our knowledge of growth and proportion in the embryo, in the new-born and in the child. The statistical tables give a complete survey of the present knowledge of the body weight, body length, limb length

and cranial measurements in the new-born and at various ages, supplemented by valuable curves. The variation of these factors is considered in relation to race, climate, clinical history of the mother, social status and placental weight. The vexed problem of the calculation of the weight in terms of sitting height is adequately discussed. The bibliography of the anthropological statistics relating to children is exhaustive and includes the most recent work in America.

The anatomy of the chest, as described by Prof. Graper, is precise but somewhat curtailed. The lymphatic glands and "dead spaces" in relation to the great veins of the thorax might have been discussed in greater detail in view of their clinical importance.

Surface Anatomy. By ARTHUR ROBINSON and E. B. JAMIESON. (Humphrey Milford, Oxford University Press.) 1928. Pp. vi + 175. 38 Figs. Price 15*s.* net.

This text-book of Surface Anatomy by two distinguished anatomists of the Edinburgh School is a typical example of the manner in which books are multiplied to no good purpose. The section dealing with Surface Anatomy in Cunningham's *Text Book of Anatomy*, written by that brilliant surgeon, Sir Harold Stiles, possesses such merit that it is hard to grasp the necessity for yet another exposition of Surface Anatomy by the Edinburgh School. Presumably one anatomical catechism is not enough for Scotland. The generous legacy of Sir Harold Stiles has been converted into a most dangerous form of cram book. Several of the diagrams are already familiar to students of the Dissecting Manual of Cunningham. The spleen and suprarenals are not figured at all, the ventricles of the brain are inadequately treated and there is a general disregard of those surface markings which have come to acquire a special significance as a result of the extended areas of the body now accessible to surgery. The pelvis is but meagrely treated.

The mandibular branch of the facial is still figured and described in relation to the mandible notwithstanding that to the surgeon it must be regarded as passing below the lower border of the mandible in part of its course. The segmental areas of the cutaneous nerves are inaccurate and the median nerve in the hand is figured as containing fibres of the fifth cervical nerve. The diagram of the cutaneous nerve supply in the lower limbs is not satisfactory and the cutaneous distribution of the obturator nerve is omitted.

Vererbung anatomischer Variationen der Nase, ihrer Nebenhöhlen und des Gehörorgans. By Dr HANS LEICHER. (Munich; Bergmann.) 1928. Pp. viii + 164. 64 Figs. and 29 Tables. Price 21 gold marks.

This contribution by Dr Leicher of Frankfurt-on-Main to Prof. Körner's monumental treatise on "Diseases of the Ear" is the most comprehensive radiological study of the normal range of variation in the anatomy of the

nose, ear, and cranial sinuses. The anthropological study of the anatomical characters of family groups of pure and mixed race is based largely on radiographic evidence and affords an excellent example of the manner in which valuable information can be collated in the living with greater speed and accuracy than by the examination of museum specimens of doubtful history. The statistical information as regards the variation in pneumatisation of the mastoid process of the frontal and maxillary sinuses is of considerable clinical importance, and confirms the figures of Cheatle, Turner, and Porter. The radiograms are excellent.

Röntgenology. The Borderlands of the Normal and Early Pathological in the Skiagram. By ALBAN KÖHLER. Translation of the fifth German edition by ARTHUR TURNBULL. (London; Baillière, Tindall and Cox.) 1928. 10″ × 7″. Pp. xvi + 556. 324 Plates and Figs. Price 42*s.* net.

Since its first appearance in 1910 the text book of *Röntgenology* by Prof. Alban Köhler of Wiesbaden has easily held first place. It owes its position to the sound anatomical arrangement, the emphasis of the range of the normal, and the prudent depiction of the early pathological states. The radiologist should know the book from cover to cover, the student should be encouraged to use it as a reference book, and the clinician, especially the surgeon, should never make a diagnosis of an apparently rare bone condition without consulting this healthy check on the overburdened terminology of the diseases of the osseous system.

The rapid development of the application of radiology to clinical practice has left but little time for the study of the normal range of variation in anatomical structure, and as yet, the physiological range is almost unknown. The changes in shape, size and consistency of the lungs and heart with changes in intrapleural pressure afford a case in point and account for the frequent conflicts between clinical and radiological reports in cases of diseases of the chest. The study of nutritional and pathological conditions in bone has hardly commenced and as yet no attempt has been made to correlate the radiographic appearance with the microscopic structure. To the anatomist and pathologist, as distinct from the radiologist and clinician, Köhler indicates how large are the gaps in the field to which he has contributed so much.

In view of the reviewer's intimate acquaintance with the fourth German edition of this work, the translator is to be warmly complimented on the manner in which he has completed his task. The future development of the subject of Radiology is of such importance that one might wish for a complete bibliography at the end of the book as distinct from the useful but scattered bibliographical data in the form of footnotes.

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